Primate Dispersal:
Proximate and Ultimate Causes
and Consequences (Part 2)

Cover Photo: Adult male (left) and female (right) Japanese macaques (*Macaca fuscata*) near an urban area. Habitat disturbance has increased the incidence of female dispersal in this species. (Photo by Fumio Fukuda).

Contents

Contents

Contents of Primate Report No. 67: Primate Dispersal: Proximate and Ultimate Causes and Consequences (Part 1).

PREFACE: THE PROXIMATE AND ULTIMATE COSTS AND BENEFITS OF DISPERSAL IN PRIMATES. JONES, C.B.

Primate units (e.g., genes, individuals, groups, populations, species) may be viewed as patches in temporally and spatially heterogeneous regimes. The study of primate dispersal entails an investigation of the motivations, causes, and consequences of movement between social groups (CLOBERT et al., 2001 a) for these units. The present special issue addresses this domain of inquiry from a variety of theoretical and empirical perspectives.

The "patch" view of physical and biotic (including social) environments, initiated by MAC ARTHUR and WILSON (1967) and LEVINS (1968; also see LEWONTIN, 1957; LEVIN, 1976) has received increased attention in recent years due to researchers' attempts to document the effects of habitat fragmentation and other anthropogenic perturbations upon plant and animal species (HANSKI et al., 1997; CLOBERT et al., 2001 b). Despite this renewed emphasis upon spatial dynamics in ecology and population biology, there has been relatively little work in primatology on the effects of spatial factors within and between populations. A search of the database, PrimateLit (http://primatelit.library.wisc.edu), yields 1,327 abstracts, articles, or books on the topic, "space" (Table 1). However, most of these publications concern the spatiotemporal distribution of mates or space as studied by experimental psychologists and neuroscientists, the latter literature reflecting the traditional social scientific origins of the discipline of primatology as well as an emphasis upon proximate mechanisms. Table 1 also documents the relative poverty of primate literature on a variety of topics related to spatial dynamics (e.g., habitat selection: see OSTRO et al., 2000; refuges: see KINZEY, 1982; JONES, 1987), although the search yielded 463 publications on the topic, "dispersal", 189 on the topic "community" (see FLEAGLE et al., 1999; JONES, 1995), and 117 on the topic "fragmentation" (see JONES, 1999).

Table 1: Results of search on PrimateLit on topics related to spatial dynamics (1940-present).

Topic	Number of Citations
Space	1,327
Dispersal	463
Community	189
Fragmentation	117
Biogeography	103
Metapopulation	7
Refuges	1
Spatial foraging	0
Models and theory	0
Patch dynamics	0

Topic	Number of Citations
Population regulation	0
Competition and space	0
Spatial ecology	0
Island biogeography	0
Habitat selection	0

From an evolutionary perspective, dispersal is of fundamental importance since it may counteract the effects of genetic drift by maintaining the connection between subpopulations and populations, preventing isolation. The papers in this special issue address dispersal at several levels of analysis, from gene to species, reflecting a concern for the benefits and costs of dispersal to the inclusive fitness of individuals, the ultimate selection pressures leading to gene flow (CLOBERT et al., 2001 a). Table 2 presents a list of proximate and ultimate factors that may lead to primate dispersal, including those factors proposed by PUSEY and PACKER (1987) in their classic review. Table 2 is not intended to be exhaustive; nonetheless, it does reflect a contemporary view that primate dispersal may have physiological and developmental, in addition to abiotic, behavioral, and social causes and consequences. In addition, Table 2 includes factors pertaining to sexual conflict (e.g., mating rates) which occurs when traits facilitating the reproductive success of one sex reduce the fitness of the other sex (see CHAPMAN et al., 2003; NUNN, 2003). Hypotheses for theoretical and empirical tests of primate dispersal can be generated from Table 2 such as that sexual conflict might drive female dispersal in some species.

Table 2: Possible proximate and ultimate causes of primate dispersal.

Proximate Factors	Ultimate Factors
Interaction rates (including mating rates)	Seek unexploited resources for conversion to offspring
Coercion	Avoid mate competition, especially with kin
Force	Avoid resource competition, especially with kin
Persuasion	Avoid inbreeding and/or areas of lower genetic heterogeneity
Attraction to extragroup individuals	Avoid other factors deleterious to survival and/or reproductive success (e.g., sexual conflict, sperm competition, increasing population size [see Gavrilets, 2000], predation, disease, infanticide, parasites, including social parasites)
Nutrition	Locate higher quality mates
Physiological factors (e.g., hormones)	Locate genetically compatible mates
Response to environmental perturbation (e.g., habitat disturbance)	Locate phenotypically compatible mates
	Locate more mates

The organization and editing of this special issue was made possible by the good-natured involvement of professionals, including the contributors, Dr. Dr. Michael Schwibbe, Editor of Primate Report, and Heike Klensang, Schwibbe's Editorial Assistant. I am very grateful for the cooperation of these individuals at all stages of the present project. I also wish to thank Dr. Rob Horwich for giving me the opportunity to study black howler monkeys (*Alouatta pigra*) at the Community Baboon Sanctuary in Belize in association with his organization, Community Conservation, Inc. (U.S.A.). I hope that this special issue will promote the study of spatial dynamics in primates, both theoretically and empirically, in order to achieve a better understanding of the spatial patterning of primate populations and the communities of which they are components.

References

CHAPMAN, T., ARNQVIST, G., BANGHAM, J. and ROWE, L.: Sexual conflict. TREE (2003) 18:41-47.

CLOBERT, J., WOLFF, J.O., NICHOLS, J.D., DANCHIN, E. and DHONDT, A.A.: Introduction. In: CLOBERT, J., DANCHIN, E., DHONDT, A.A. and NICHOLS, J.D. (eds.): Dispersal. Oxford: Oxford University Press (2001 a): xvii-xxi.

CLOBERT, J., DANCHIN, E., DHONDT, A.A. and NICHOLS, J.D. (eds.): Dispersal. Oxford: Oxford University Press (2001 b).

FLEAGLE, J.G., JANSON, C. and REED, K.E. (eds.): Primate Communities. Cambridge: Cambridge University Press (1999).

GAVRILETS, S.: Rapid evolution of reproductive barriers driven by sexual conflict. Nature (2000) 403: 886-889.

HANSKI, I.A. and GILPIN, M.E. (eds.): Metapopulation Biology: Ecology, Genetics, and Evolution. New York: Academic Press (1997).

JONES, C.B.: Evidence supporting the Pleistocene forest refuge hypothesis for Primates. Biotropica (1987) 19: 373-375.

JONES, C.B.:The potential for metacommunity effects upon howler monkeys. Neotropical Primates (1995) 3: 43-45.

JONES, C.B.: Why both sexes leave: Effects of habitat fragmentation on dispersal behavior. Endangered Species Update (1999) 16: 70-73.

KINZEY, W.G.: Distribution of primates and forest refuges. In: PRANCE, G.T. (ed.): Biological Diversification in the Tropics. New York: Columbia University Press (1982): 455-482.

LEVIN, S.A.: Population dynamics models in heterogeneous environments. Ann. Rev. Ecol. Syst. (1976) 7: 287-310.

LEVINS, R.: Evolution in Changing Environments. Princeton: Princeton University Press (1968).

LEWONTIN, R.C.: The adaptations of populations to varying environments. Cold Spring Harbor Symp. Quant. Biol. (1957) 22: 395-408.

MAC ARTHUR, R.H. and WILSON, E.O.: The Theory of Island Biogeography. Princeton: Princeton University Press (1967).

NUNN, C.L.: Comparative and theoretical approaches to studying sexual selection in primates. In: JONES, C.B. (ed.): Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions. Norman, OK: American Society of Primatologists (2003): 593-613.

OSTRO, L.E.T., SILVER, S.C., KOONTZ, F.W. and KOONTZ, T.P.: Habitat selection by translocated black howler monkeys in Belize. Animal Conservation (2000) 3: 175-181.

PUSEY, A.E. and PACKER, C.: Dispersal and philopatry. In: SMUTS, B.B., CHENEY, D.L., SEYFARTH, R.M., WRANGHAM, R.W. and STRUHSAKER, T.T. (eds.): Primate Societies. Chicago: University of Chicago Press (1986): 250-266.

Correspondence to:
Dr. Clara B. Jones, *Livingstone College, School of Liberal Arts, 701 W. Monroe Street, Salisbury, NC 28144, U.S.A.; E-mail:* cjones@livingstone.edu; howler425@cs.com.

THE NUMBER OF ADULT FEMALES IN GROUPS OF POLYGYNOUS HOW-
LING MONKEYS (*ALOUATTA* SPP.): THEORETICAL INFERENCES.
JONES, C.B.

Key Words: *Alouatta*, polygynous howling monkeys, female primates, game theoret-
ical models, resource dispersion hypothesis, reproductive skew

Abstract

Several reports have documented that adult female group size in polygynous
howler monkey (*Alouatta*) species rarely exceeds 4. This paper evaluates three sche-
mas for the interpretation of this phenomenon: (1) a simple game theoretical model;
(2) the resource dispersion hypothesis; and, (3) certain models of reproductive skew.
Similarities among these schemas are noted, and their possible utility in explaining
differences between the typically polygynandrous *A. palliata* and typically poly-
gynous species of the genus is discussed. Suggestions for future research are pro-
posed, including data required to test each schema.

Introduction

Howlers (*Alouatta* spp.), members of the Neotropical family Atelidae, are distrib-
uted from southern Mexico to northern Argentina (GROVES, 2001; RYLANDS et
al., 2000; CROCKETT and EISENBERG, 1987). All species studied are structured
into highly communal groups residing on home ranges defended by vocal advertise-
ment, and social organization is notably flexible, characterized by variation in the
number of adult males within groups (CROCKETT and EISENBERG, 1987) and by
the tendency to form sub-groups (KINZEY and CUNNINGHAM, 1994; JONES,
1995a, b; CROCKETT, 1998; CROCKETT and EISENBERG, 1987). Howlers adapt
well to a broad range of habitats, disturbed or undisturbed, though, because these
wholly vegetarian monkeys are almost exclusively arboreal, habitat disturbance, in-
cluding fragmentation, can threaten their survival (CROCKETT, 1998). Compared
to many other primate taxa (e.g., some species of *Macaca* and *Papio*), overt conflict is
thought to be uncommon in howlers (e.g., CARPENTER, 1934; JONES, 1980, 2000;
MENDES, 1989; SILVEIRA and CODENOTTI, 2001), and, of the direct agonism ob-
served (e.g., chases, fights), several authors have noted that it is more common
among adult females than among adult males (JONES, 2000; GIUDICE, 1993; also
see CARPENTER, 1934; ZUCKER and CLARKE, 1998). Communication is primari-
ly vocal in howlers (WILSON, 1975; CARPENTER, 1934; ALTMANN, 1959; JONES,
1980 2000; SILVEIRA and CODENOTTI, 2001), leading some authors to suggest
that this genus provides a rich model for the evolution of social behavior (WILSON,
1975; CROCKETT, 1987; EISENBERG, 1991).

While a significant degree of variability exists in primate sociosexual organiza-
tion (DIXSON, 1998), most species live and reproduce in social groups including at
least one adult male, one adult female, and their offspring. Following DIXSON's
(1998) classification, "polygynous" primates are characterized by those species hav-
ing one reproductive male and one or more reproductive females per group. GRO-

VES (2001) describes eight howler species confirmed to have a modal polygynous social structure. The present paper discusses adult females of four of these species: *A. seniculus* (the red howling monkey), *A. pigra* (the black howling monkey), *A. caraya* (the black and gold howling monkey), and *A. guariba/A. fusca* (the red-and-black howling monkey). None of the polygynous species has been studied as thoroughly as the congeneric mantled howling monkey (*A. palliata*), whose modal sociosexual organization is polygynandrous (multimale-multifemale). In this paper, an attempt is made to evaluate three schemas pertaining to adult female group size and dispersal in polygynous howlers: (1) a simple game theoretical formulation; (2) the resource dispersion hypothesis [RDH]; and, (3) certain reproductive skew models. Additionally, I will attempt to highlight the data required to resolve unanswered questions. In the following, "female group size" pertains to group size of *adult* females.

Adult Female Group Size in Polygynous Howlers and its Relationship to Dispersal

A female's tactics and strategies to optimize lifetime reproductive success will be constrained by her energetic requirements (SCHOENER, 1971), including her initial investment in the size and cost of gametes (TRIVERS, 1972). Females are expected to adopt those behavioral programs conferring the most advantageous benefit to cost ratio from the conversion of resources, especially food, into offspring (EMLEN and ORING, 1977; BRADBURY and VEHRENCAMP, 1977; WRANGHAM, 1980; SILK, 1993; WITTENBERGER, 1980). In density-dependent conditions, the availability of energy will ultimately limit group size (WILSON, 1975; WITTENBERGER, 1980); however, modal population structure (i.e., whether "dispersed", "polygynous", or "multimale-multifemale" groups occur) is thought to be a function of resource distribution, abundance, monopolizability, and quality in time and space (see review in HORWICH et al., 2001, pp. 47-49). Other factors may also influence population structure such as predation, male agonism, or habitat saturation (VAN SCHAIK, 1983; CROCKETT and JANSON, 2000; EMLEN, 1995; STERCK et al., 1997; JOHNSON et al., 2002). The relative importance of these factors for female group size is disputed in the primate literature (e.g., CROCKETT and JANSON, 2000; ISBELL and YOUNG, 2002; STERCK et al., 1997).

Several authors have noted a remarkable feature of female groups in polygynous howlers: population surveys document that female group size rarely exceeds 4 (CROCKETT and EISENBERG, 1987; CROCKETT and POPE, 1993; CROCKETT, 1996; CROCKETT and JANSON, 2000; HORWICH et al., 2001; *A. seniculus*: RUDRAN, 1979; IZAWA, 1992; see CROCKETT, 1996; *A. pigra*: HORWICH et al., 2001; OSTRO et al., 1999; OSTRO et al., 2001; LOPEZ and RUMIZ, 1995; BOLIN, 1981; ESTRADA et al., 2002a,b; *A. caraya*: THORINGTON et al., 1984; RUMIZ, 1990; GIUDICE, 1993; G.E. ZUNINO, personal communication (p.c.), April 2000; *A. fusca* [*A. guariba*]: da SILVA, 1981; MENDES, 1989). For *A. caraya*, female group size > 4 appears most likely to occur on islands where populations are likely to be saturated (Isla Guascara, Argentina: RUMIZ, 1990; Isla Brasilera, Argentina: G.E. ZUNINO, p.c., April 2000). HORWICH et al. (2001, p. 53) concluded that "adult female group size in polygynous howling monkeys is highly conserved", and CROCKETT and JANSON (2000, p. 90), discussing *A. seniculus*, proposed that patterns of dispersal are "directly related to the number of adult females already present in the natal troop".

In 1975, WILSON argued that group size results from factors leading individuals to join and to leave groups combined with the selection pressures on individual responses to these forces. Thus, determining the costs and benefits of emigration and immigration to howler females who have attained group membership compared to those seeking group membership should reveal, in part, the causes of their conservative group size. Because maximum female group size is ≈4 in all species of polygynous howlers studied to date, the factors accounting for this phenomenon are proposed to be the same in each case. Female-female competition for group membership, and subsequent access to limited breeding positions, may be the ultimate explanation for conservative female group size in polygynous howlers (CROCKETT and EISENBERG, 1987; CROCKETT, 1984; see JONES, 1980), and dispersal is thought to be the proximate mechanism underlying the limitation of female numbers in these groups (CROCKETT and EISENBERG, 1987).

Female dispersal has been documented in several species of polygynous howlers (*A. seniculus*: CROCKETT, 1984; *A. pigra*: BROCKETT et al., 2000, and references; *A. caraya*: CALEGARO-MARQUES and BICCA-MARQUES, 1996), and both sexes of howling monkeys emigrate from their natal groups as juveniles (CROCKETT and EISENBERG, 1987; JONES, 1978, 1980; GLANDER, 1992; CROCKETT and POPE, 1993; see PUSEY and PACKER, 1987). While "secondary dispersal" is rare or absent in most howler societies (GLANDER, 1992), adult females may emigrate from groups (GLANDER, 1992; JONES, 1980), and ejection (i.e., expulsion from the group by another member of the same sex ["targeting": STERCK et al., 1997]) appears to be an important mechanism leading to the egress of females from howler groups (JONES, 1980; CROCKETT, 1984; BROCKETT et al., 2000). Howler females, then, may be forced by other females to leave groups independent of the costs associated with emigration (see CROCKETT and POPE, 1993, p. 117), and probabilities of ejection entail (predictable?) costs associated with group membership for female howlers.

A Simple Game Theoretical Model of Female Dispersal in Howlers

GROSS (1996; also see WEST-EBERHARD, 1979) argued that social interactions drive individual phenotypic variation within the sexes and that game theory and the evolutionarily stable strategy (ESS) concept may be utilized to analyze "how and why selection favours alternative phenotypes" (p. 92). Fig. 1 (based on PULLIAM and CARACO, 1984) displays a hypothetical two-individual (two-female) game. Each female is presumed to be acting selfishly to optimize individual fitness, and female 1 may be regarded as dominant to female 2 where female 1 is the actor with greater resource holding potential (PARKER, 1974) at the time of the interaction. This view implies that rank may be density- and/or frequency-dependent, possibly sensitive to interaction rates, and that rank may vary over time and space (see GROSS, 1996). In general, dominants are presumed to accrue higher relative fitness for the period of time that the interactions persist. However, "role reversal", whereby the subordinate wins a contest with the dominant and the dominant subsequently becomes subordinate, or ejection of the dominant may occur (CANT and JOHNSTONE, 2000), especially where the subordinate has more to gain by winning than the dominant has to lose (PARKER, 1974; see JONES, 1980, p. 400). As pointed out by CANT and JOHNSTONE (2000), agonistic interactions between two individuals

may have one of three outcomes: (1) the loser may be killed (an outcome that has not been reported for female howlers); (2) the loser may be evicted, a documented effect for female howlers (see references above) and modeled in Fig. 1; or, (3) the loser becomes (or remains) subordinate, an outcome also documented for female howlers

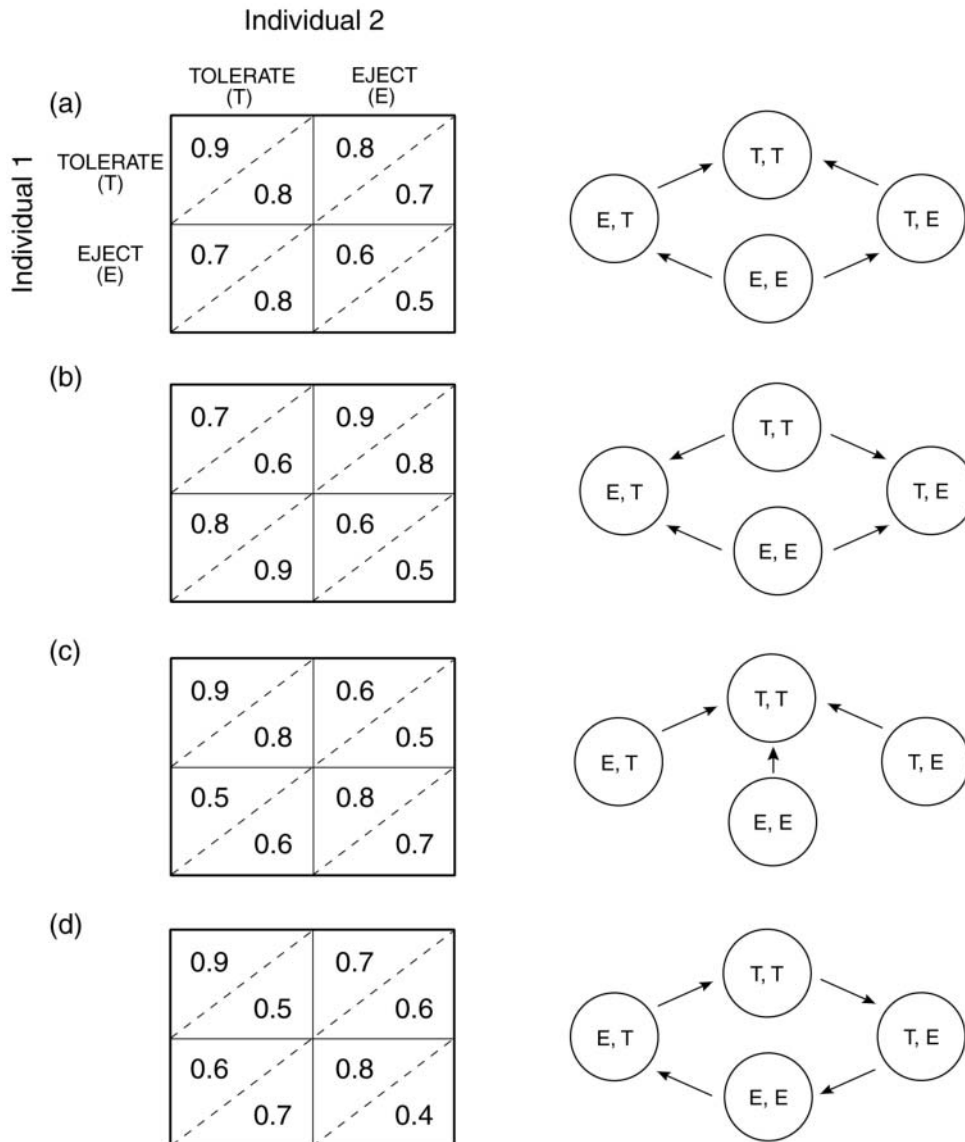Fig. 1: A two-person game displayed as a payoff matrix in each of four (hypothetical) conditions (based on PULLIAM and CARACO, 1984, Fig. 5.4). Rows and columns are controlled by individual (female) 1 and individual (female) 2, respectively. Transition graphs are displayed to the right of each payoff matrix showing expected outcomes if individuals make decisions optimally. See text for further explanation.

(see references above) and modeled in Fig. 1. Fig. 1 may also be viewed as a game between kin whose decisions will be sensitive to the intensity of competition in different environmental regimes (see PEREZ-TOME and TORO, 1982; WEST et al., 2002).

Fig. 1 illustrates the straightforward example of two females interacting, say, contesting the resource "group membership" or "breeding position", with two possible strategies (condition-dependent behavioral phenotypes: see GROSS, 1996), tolerate (T) or eject (E). If T, then it is in the interest of an individual to tolerate another in the group. If E, then it is in the interest of an individual to eject her rival from the group. The four matrices in Fig. 1 (a-d) display different (hypothetical) fitness values in four states (e.g., competitive regimes). In each cell of each matrix, the number above the diagonal refers to the relative fitness of female 1, and the number below the diagonal refers to the relative fitness of female 2. These matrix "payoff" values can represent fitness in the general sense ("inclusive fitness") resulting from the benefits and costs of female group membership (i.e., access to group membership and/or breeding positions) as well as fitness benefits and costs in rates of food intake, predator detection and defense, protection from infanticide, access to mates, and the like (see WEST et al., 2002).

Decisions, not necessarily conscious, are presumed to be those strategies reflecting individual self-interest. In each condition, four outcomes are possible: T, T where both females decide to tolerate each other in the group. This outcome should yield no agonism or low levels of agonism between females because it is in the interest of both females to tolerate each other in the group. For the second possible outcome, T, E, it is in the interest of female 1 to tolerate female 2 and in the interest of female 2 to eject female 1. Female 1 may decide to tolerate female 2 because of benefits related to assistance in predator defense or foraging, or kinship, for example. It may, however, be in the interest of female 2 to eject female 1 as a result of "dominance testing" (CANT and JOHNSTONE, 2000) or interference competition. In this situation, if female 2 is subordinate to female 1, female 2 may attempt coalitions or alliances with other females to eject female 1. While such coalitions have been documented for *A. palliata* females (JONES, 1980, 2000), they have not been reported for female howlers of polygynous species. Nonetheless, this condition may lead to conflict, yielding agonistic interactions among females. With this outcome, female-female agonism, whether direct or indirect, may not be intense, since, as reflected by the fitness values for each female in this cell of the four matrices, female 1, the presumed dominant, has the advantage in pairwise interactions.

For the third possible outcome, E, T, it is in the interest of female 1 to eject female 2 but in the interest of female 2 to tolerate female 1, possibly because of low likelihoods of finding a breeding position elsewhere (see EMLEN, 1995). In this condition, female 2, the presumed subordinate, will have more to gain than female 1 has to lose (PARKER, 1974; see JONES, 1980, p. 400); thus, female 2 is expected to expend greater relative effort in retaining group membership and, thus, a breeding position. While female-female agonism is expected with this outcome, it may not be intense since conflicts may be settled quickly, either because the dominant has greater fighting ability relative to the subordinate or because the dominant assesses the subordinate's willingness to invest more in winning, leading to "role reversal", where the dominant becomes a subordinate within the group, or ejection of the dominant (fe-

male 1) from the group (CANT and JOHNSTONE, 2000). Alternatively, where it pays the subordinate (female 2) to invest more in winning, the dominant (female 1) may form coalitions or alliances with other subordinates to defeat female 2.

For the fourth possible outcome, E, E, it is in the interest of both individuals to eject the other, possibly because of mutual interference or other disadvantages (e.g., increased likelihood of infanticide: CROCKETT and JANSON, 2000). This condition may be reflective of the situation for polygynous female howlers when maximum group size has been attained, whatever the precise factors making a group size no more than 4 advantageous. Again, as the fitness values within this cell in all four matrices indicate, female 1, the presumed dominant, has the advantage; however, female-female agonism under these conditions is expected to be intense, and, as for the third outcome, may be a function of fighting ability of the dominant or level of investment ("motivation") by the subordinate. For the second, third, and fourth possible outcomes, the frequency, rate, intensity, and duration of agonism between interacting females is expected to be a function of the total number of adult females in the group, total group size, coefficients of relatedness within groups, the rank difference between females, the likelihood of damaging encounters, as well as other factors (e.g., the clumping and monopolizability of patchy and ephemeral food or other limiting resources). Further, females of different rank may have different optimal group sizes, another factor that may produce female-female conflict and that may influence the relative fitness values for each matrix in Fig. 1.

Fig. 1 also displays a "transition graph" to the right of each matrix showing changes in decisions (displayed within circles) based upon payoff values from one cell to another. In Fig. 1a, only strategy T, T is stable (i.e., no other strategy can invade it, as indicated by the convergence of arrows upon T,T in this transition graph). In Fig. 1b, both E, T and T, E are stable, and arrows in the transition graph for this matrix converge on these two options. In Fig. 1c, only T, T is stable, as indicated by the convergence of arrows on T,T in the transition graph. Finally, in Fig. 1d, no stable equilibrium exists, and arrows converge on none of the four possible combinations. Following PULLIAM and CARACO (1984), transition graphs assume only that (1) each individual (female) has sampled the four possible states and processes values of their relative benefits and (2) an individual (female) switches her decision only if higher relative benefits can be obtained by doing so (see GROSS, 1996; WEST-EBERHARD, 1979). Fig. 1 can thus be said to display "perfect information decision rules".

The transition graphs can be described in greater detail. Fig. 1a demonstrates an equilibrium only when both females decide to tolerate each other. Thus, either female benefits from a switch to T from any other state. Once one female decides upon T, the other will do the same, since either gains from such a choice (see fitness values in matrix). In the final result, once both females have chosen T, the condition is preserved as long as any further move results in lower relative individual fitness for either female.

In Fig. 1b, the costs of T outweigh the benefits (i.e., T, T accrues a lower fitness value than E, T or T, E, as seen in the payoff matrix). Either female thus benefits from a decision to eject the other (E) when the other female is in state T. Therefore, whenever both females are interacting, the only stable equilibrium occurs when one female chooses T and the other, E (i.e., either E, T or T, E).

Figure 1c displays a state like Fig. 1a whereby the benefits of T outweigh the costs (i.e., the highest benefits to each female accrue when both tolerate each other, as shown in the payoff matrix). In this state, however, when both females choose E (i.e., E, E), T fails to pay more, as long as the other retains her choice. However, both females benefit by a decision to tolerate each other (T, T). Thus, following PULLIAM and CARACO (1984), state T, T is a "cooperative" (Pareto) equilibrium.

Fig. 1d displays a case for which no stable equilibrium exists. The consequence of such an unstable equilibrium is a "round-robin" (PULLIAM and CARACO, 1984) whereby female 1 chases female 2 from situation to situation. As PULLIAM and CARACO (1984) point out, such round robins follow from optimal decision rules whenever one individual (female) always benefits from one tradeoff and the other always benefits from an alternative one (e.g., in the matrix for Fig. 1d, no matter what decision one female makes, the other female can always do better with an alternate one). Conflicts of interindividual interest may be particularly intense under these conditions (PULLIAM and CARACO, 1984) and may exist for female howlers in polygynous species where competition is of the "scramble" variety (see CROCKETT and JANSON, 2000; also see STERCK et al., 1997), such as where limiting resources, particularly food, are ephemeral and unmonopolizable (see JONES, 1996; JONES and CORTES-ORTIZ, 1998).

Fig. 1 represents a model showing how female group size might be limited by female-female interactions, in particular, tendencies to eject or to tolerate other females in varying conditions. CROCKETT and EISENBERG (1987, p. 67; also see CROCKETT, 1984; HORWICH et al., 2001) concluded that "female emigration" characterizes howlers and that "female-female competition is a mediating factor". Fig. 1 assumes that group membership and consequent breeding positions are limiting resources for females of polygynous howler species, resources for which females might compete if it is in their interest to do so. The howler literature supports the view that females experience intense competition for group membership and, consequently, breeding positions within groups (JONES, 1978, 1980; CROCKETT, 1984; CROCKETT and JANSON, 2000). Fig. 1, then, provides a proximate explanation for variations in the number of adult females in groups of polygynous howlers.

The Resource Dispersion Hypothesis (RDH) and Female Group Size in Howlers

Alternative behavioral phenotypes such as those described in Figure 1 permit individuals to adapt to spatially and temporally heterogeneous regimes (biotic, including social, and abiotic; see GROSS, 1996). Since females are "energy maximizers" (SCHOENER, 1971; also see SILK, 1993) and since the availability of energy will ultimately limit group size (WILSON, 1975; WITTENBERGER, 1980), it seems parsimonious to conclude that female group size in polygynous howlers is a primary function of variation in food resources where populations occur in density-dependent conditions (WITTENBERGER, 1980). The RDH predicts that the temporal and spatial dispersion, abundance, and quality of resources lead animals to accrue a larger territory or home range than required for survival and reproduction because an area large enough to encompass unpredictable patterns of resource availability is needed (JOHNSON et al., 2002). These larger areas, accrued in response to the patchiness of resources, yield an excess of resources, permitting the coexistence of secondary animal(s) without loss of fitness for the primary (JOHNSON et al., 2002).

For our present discussion of dispersal and its relationship to female group size in polygynous howlers, it is the *temporal* component of the RDH that is of most concern since theory predicts that mammals are most likely to disperse, or, possibly, be ejected from, their resident groups in the face of temporal environmental variation (JOHNSON and GAINES, 1990). While the RDH makes no specific predictions about group size (JOHNSON et al., 2002), it follows from these authors' arguments that group size will be a function of the richness and dispersion of resources within patches. JOHNSON et al. (2002) point out that support for the RDH may derive from a demonstration that group size and home range size are uncorrelated. While few data exist to test this relationship for polygynous howlers, preliminary reports indicate that group size and home range size are uncorrelated in most cases (*A. pigra*: OSTRO et al., 1999; *A. caraya*: ZUNINO et al., 2001; G.E. ZUNINO, personal communication, December 2002; also see SEKULIC, 1982, for *A. seniculus*).

Tolerance of secondary females by primary females may be viewed as a form of reproductive incentive to secondaries to remain in the group. This view assumes that the fitness of the primary female is not decreased below some threshold value by the addition of one or more secondary females and that there are costs to dispersal yielding benefits from group membership to the secondary female (JOHNSON et al., 2002). Ejection would be favored where costs (to inclusive fitness) exceed some threshold value for the primary female (see WEST et al., 2002). The RDH leads to the conclusion that small female group sizes in polygynous howler species result from relatively less resource heterogeneity compared to mantled howlers for whom high resource heterogeneity may increase environmental unpredictability and impose high costs of eviction to primary females, outweighing the benefits of evicting secondaries. One advantage of the RDH approach is that it explains the formation and maintenance of groups without a need for explanations dependent upon "functional benefits" (e.g., predator defense, risk of infanticide, competition for food: JOHNSON et al., 2002, p. 564). An inference from the RDH combined with dispersal theory is that the *temporal* heterogeneity of food will favor female dispersal in polygynous howlers.

Dispersal and Reproductive Skew in Groups of Polygynous Female Howlers

In the RDH, an incentive to stay in the group can be any factor making group life beneficial to the secondary animal, whether provided directly by the primary animal or not (JOHNSON et al., 2002). Related to this, "staying incentives" to subordinates by dominants are central to many discussions of reproductive skew (the apportionment of reproduction within groups: e.g., REEVE and EMLEN, 2000; CANT and JOHNSTONE, 2000). First, in skew theory's "concession" models (e.g., REEVE and EMLEN, 2000), an incentive is defined as a share of reproduction (total group [reproductive] productivity) conceded to the subordinate by the dominant. Incentives are theorized to induce the subordinate to remain in the group and, since it is the dominant who "decides" to yield or not to yield a staying incentive (e.g., group membership or a breeding position), the dominant ultimately determines group size (REEVE and EMLEN, 2000).

Dominant female howlers may employ at least two incentives pertinent to the present discussion: (1) allowing a subordinate female to achieve membership in the group and (2) allowing a subordinate to breed in the group. Because of the character-

istic "age-reversed" dominance hierarchies found in howlers (JONES, 1978, 1980, 1983) and because reproductive suppression of subordinates by dominants apparently does not occur in howlers (see STRIER, 2001), both incentives have, essentially, the same consequences and will be treated here interchangeably. It is important to note, however, that, in groups of unrelated individuals, "the staying incentive decreases with increasing [group size]; in particular, the staying incentive always decreases with increasing group size if the relatedness is zero" and solitary output (the reproductive output of a solitary breeder) is greater than zero (REEVE and EMLEN, 2000, p. 643). Thus, for polygynous female howlers whose relatedness to other group members may be low because of dispersal patterns, staying incentives (opportunities for breeding within the group) are expected to decrease as group size approaches the saturation point (the point at which strategy E (Fig. 1) benefits the dominant: REEVE and EMLEN, 2000), if the subordinate's reproductive potential is > 0.

Saturated group size will be determined by local (patch) conditions, explaining why group size for polygynous female howlers does not always reach 4 since patches may vary in their capacity to sustain individuals, affecting the tradeoffs to individuals of staying, leaving, or ejecting. It is not clear whether studies of polygynous howlers reporting female group sizes < 4 represent unsaturated groups (group sizes for which T benefits the dominant: REEVE and EMLEN, 2000) or groups whose saturation size is < 4 (group sizes for which T (Fig. 1) is unbeneficial to the dominant). As REEVE and EMLEN (2000, p. 645) point out, empirical tests of theoretical predictions of concession models "requires knowledge of whether groups are or are not saturated". Future research on female group size in howlers needs to address this issue, possibly with field experiments manipulating the number of females in groups and measuring the strategies of dominants before and after manipulation. Such studies would require empirical assessment of ecological constraints (i.e., the likelihood of solitary breeding), group productivity, and average relatedness within groups (r).

Where r within groups is low, as it is thought to be for howlers (see POPE, 1992; JONES, 1995c), REEVE and EMLEN'S (2000) model describing group size in saturated groups predicts that decreases in group size will occur by ejection of subordinates by dominants or, less commonly, by other subordinates. Since ejection ("targeting": STERCK et al., 1997) is apparently characteristic of howlers, it follows that concession models should be very helpful in understanding howler behavior and social organization as well as other primate species exhibiting ejection. Importantly, CANT and JOHNSTONE (2000) point out that it is critical for empirical studies to document who initiates agonistic interactions in order to resolve questions concerning the apportionment of incentives, and REEVE and EMLEN (2000) stress the significance of assessing the costs of eviction to dominants.

Following CANT and JOHNSTONE (2000, p. 406), skew theory predicts that "The size of...staying incentives is predicted to decrease (and reproductive skew to increase) according to three factors: first, the extent to which opportunities for independent breeding are constrained by ecological factors; second, the extent to which the presence of a subordinate increases the productivity of the group; and, third, the relatedness between dominant and subordinate". Each of these factors will be discussed briefly in turn. Nothing is known of reproductive skew in polygynous howlers, although female *A. seniculus* are unable to breed successfully outside a group

(CROCKETT and JANSON, 2000). This finding most likely applies, as well, to other howlers (e.g., *A. pigra*, *A. palliata*, C.B. Jones, personal observation). Numerous surveys of polygynous howlers document that a reproductive unit may comprise only one reproductive male and one reproductive female (see references above). HORWICH et al. (2001, pp. 58-59), studying *A. pigra*, found that 16 % of the groups in their sample contained just one adult male and one adult female. These authors argued, however, that, because relative reproductive success (RRS: the mean number of immatures:females per female group size) decreased with an increase in female group size, reproductive rates were highest in one-female reproductive units. HORWICH et al. (2001) suggested that, while a female group size of one may be optimal for female fecundity, it may be unstable because of environmental heterogeneity, inefficient predator detection, or other factors. Whatever the reality turns out to be, skew theory predicts that smaller group sizes are associated with "relaxed" ecological constraints (REEVE and EMLEN, 2000), consistent with BOLIN's (1981) findings for Belizean *A. pigra* after a major storm had decimated the population, presumably yielding opportunities for independent reproduction by females.

Ecological effects may constrain the breeding of subordinate females if they are impacted to a greater degree by the effects of environmental heterogeneity, in particular, temporal environmental heterogeneity. In general, skew theory predicts that high skew will be correlated with "severe" ecological constraints while low skew will be correlated with "weak" ecological constraints (CANT and JOHNSTONE, 2000; REEVE and EMLEN, 2000). Thus, it is expected that polygynous female howlers in conditions of high population density (e.g., *A. pigra*: OSTRO et al., 2001; HORWICH et al., 2001, Table 1) would exhibit high skew while polygynous female howlers in conditions of low population density (e.g., *A. pigra*: BOLIN, 1981; see OSTRO et al., 2001; HORWICH et al., 2001, Table 1) would exhibit low skew. REEVE and RATNIEKS (1993) showed further that no incentives at all are required if ecological constraints are very severe (i.e., no opportunities for independent reproduction, for example, through colonization). As noted above, dominant howler females have not been shown to suppress the reproduction of subordinates; thus, this possibility appears unlikely, probably because, in groups of unrelated females, benefits from indirect reproduction (assisting the reproduction of kin) would be low (but see WEST et al., 2002). In sum, where howler females experience intense ecological constraints (i.e., low opportunities for independent breeding leading to intense competition for group membership and, consequently, breeding positions within groups), then skew is expected to be high. Following CANT and JOHNSTONE (2000), groups are expected to form only where ecological constraints are moderate to high.

Concerning CANT and JOHNSTONE's (2000) second factor, no study of polygynous howlers has measured the extent to which a subordinate may increase group productivity, although factors reducing group productivity (e.g., agonism by subordinates) are expected to increase skew (see CANT and JOHNSTONE, 2000, pp. 408-409). HORWICH et al.'s (2001) demonstration that RRS decreased significantly with increasing female group size showed that, as group size increased, group productivity decreased. CROCKETT and JANSON (2000, p. 90), utilizing different methods than in the *A. pigra* study, found that "larger group size may depress birth rate" for *A. seniculus*; however, their result was not significant. Assuming that the addition of a subordinate benefits the primary female of a one-female group (e.g., by

increasing survivorship of the primary by increased efficiency in predator detection or foraging), these results suggest that there exists a threshold at a saturated group size no more than ≈4 whereby these advantages begin to decrease. This threshold may occur for females of polygynous howler species where environmental heterogeneity of limiting resources increases beyond some threshold value that is difficult for females to predict. The optimal response for dominant female howlers in polygynous species may be to eject subordinate females, possibly in response to interaction rates, constricting group size (see Figure 1, b and d) and enhancing competition for breeding positions within a population.

Considering CANT and JOHNSTONE's (2000) third factor, due to the effects of dispersal, as stated above, average *r* is expected to be low in female groups of polygynous howlers, although precise values of *r* for female groups have not been reported (but see POPE, 1992). CANT and JOHNSTONE (2000, p. 413) predicted that "increasing relatedness favors high skew and [lower levels of aggression]". Thus, polygynous female howlers in groups with low average *r* are expected to show lower levels of skew and higher rates of aggression, all other things being equal, than comparable females in groups with higher average *r*.

Assessing the import of group size for reproductive skew, REEVE and EMLEN (2000, pp. 643-644) showed that "the sensitivity of the staying incentive to relatedness will decline with increasing size". Thus, as female group size increases from 2 to ≈4 for polygynous howlers (depending upon saturated group size), the relationship between staying incentive and *r* becomes less important. These authors go on to state, "when relatedness is zero, one would expect low solitary outputs [i.e., solitary reproductive potential] to be associated with large saturated group sizes and high skews, whereas high solitary outputs would be associated with small saturated group sizes and low skew" (p. 643). Again, the saturation threshold will vary with particular local (patch) conditions, determining the precise outcomes of the relationships between ecological constraints, group productivity, and relatedness. REEVE and EMLEN (2000; also see WEST et al., 2002) showed, however, that the dominant will be more sensitive to average *r* and that, in general, the role of ecological constraints in determining skew will be more important than the role of relatedness.

A Comparative Note on Female Groups of A. palliata

The typical polygynandrous population structure of mantled howling monkeys differs significantly from its polygynous congeners (e.g., CROCKETT and EISENBERG, 1987), and CROCKETT and POPE (1993) suggest that *A. palliata* may be "less territorial than" polygynous howlers, may be more likely to form subgroups than to limit female group size in response to low-density and clumped resources, and may exhibit "reduced male-male competition" compared to polygynous howlers. Can concession models yield insights into these differences? As noted above, all howler species exhibit ejection by dominants of subordinates and, possibly, of subordinates by other subordinates. JONES (1978, 1980, 2000) demonstrated that coalitions may be formed between dominant and subordinate female mantled howlers to eject a female subordinate; however, the initiator of these coalitions was not determined. A characteristic feature of mantled howler groups compared to groups of polygynous howlers is that mean group size is greater for *A. palliata* (CROCKETT and EISENBERG, 1987; CHAPMAN et al., 1998). Since concession models predict

that large saturated group sizes and high skews are associated with low solitary outputs, it is expected that, in general, ecological constraints would be greater for mantled howler females than for females of polygynous howler species. It is not clear whether the responses of *A. palliata* compared to its congeners is likely to be—or was likely to have been over evolutionary time—more sensitive to the mean or variance of ecological constraints. However, preliminary evidence does support the present prediction, since mantled howlers at Hacienda La Pacifica are more likely to immigrate into existing groups (GLANDER, 1992; see JONES, 1980) while Venezuelan red howlers are more likely to colonize open habitat (POPE, 1992; CROCKETT and POPE, 1993).

Concession theory also predicts that the staying incentive is directly related to the success of solitary breeding and that "the staying incentive should *always* decline with increasing group size for groups of non-relatives ($r= 0$)" (REEVE and EMLEN, 2000, p 645 [emphasis in original]). Thus, it is expected that mantled howler females are less likely to tolerate other females (offer incentives in the form of breeding positions in the group) than are females of polygynous howler species. Indirect evidence supports this prediction since the frequency of agonism by mantled howler females is noteworthy (JONES, 2000; also see ZUCKER and CLARKE, 1998) while that of Belizean *A. pigra* is not (BROCKETT et al., 2000; but see GIUDICE, 1993 for *A. caraya*). If female mantled howlers are comparatively less tolerant of one another (less likely to offer incentives and more likely to be agonistic) than their congeners, then this prediction of skew theory may explain why adult males of this species have been observed to assist the entry of young females into groups (GLANDER, 1992). REEVE and EMLEN (2000) suggest ways in which skew theory might be tested, and future studies of howlers should assess differences within the genus in relation to the predictions of concession theories (e.g., REEVE and RATNIEKS, 1993; REEVE and EMLEN, 2000; see HAGER, 2003).

Finally, REEVE and EMLEN (2000) conclude that groups of non-relatives may generally be larger than groups of relatives, leading to the prediction that average r may be lower in groups of female mantled howlers than in groups of polygynous female howlers. PUSEY and PACKER (1987) point out, however, that r is expected to decrease with an increase in group size; thus, causal factors may be obscured by the larger mean group size of mantled howlers. While data to test this prediction in a tentative way for howlers are unavailable, POPE (1992) showed that, for *A. seniculus* in Venezuela, "the breeding females within an established troop eventually come to form a single matriline" (p. 1117). Her pattern of results may apply to females of other polygynous howler species, possibly explaining, in part, differences between *A. palliata* and its congeners, as well as intraspecific and interspecific differences of polygynous howlers. Models of reproductive skew have been applied most thoroughly to insect societies and to cooperative breeders; thus, caution is indicated when using these models for an analysis of most primate species. In particular, intersexual interactions (e.g., mate choice and male agonism) may be as important as intrasexual ones (KOENIG and HAYDOCK, 2001) in determining the partitioning of reproduction within groups and group size, as observations for mantled howlers suggest (JONES, 1985; JONES and CORTES-ORTIZ, 1998). Other formulations, such as "limited control" models in which the dominant's control of group productivity is incomplete (CLUTTON-BROCK, 1998), may provide a more realistic in-

terpretation of primate societies. Nonetheless, as initially pointed out by HAGER (2003), concession models of reproductive skew provide an initial attempt to dissect the causes, consequences, and dynamics of female relations in primates.

Conclusion

The present paper exhibits three related schemas for interpreting (adult) female group size in polygynous howling monkeys: a simple game theoretical framework, the RDH, and concession models of reproductive skew. The invariant property shared by each schema is that a primary female (generally, the dominant) will tolerate or not tolerate (eject) a secondary female relative to her (the primary's) self-interest. The game theoretical approach shows that such decisions will be based upon the relative fitness values of making one or the other decision—as a function of the choices that other females make. In the RDH, decisions are a function of the temporal and spatial heterogeneity of resources whose dispersion and quality determine whether or not a home range can support one or more secondary females without a cost to the primary's fitness. This approach has the advantage of not requiring functional explanations (e.g., benefits in terms of infanticide risk, predator defense, or competition for food) to explain female group size. Concession models of reproductive skew lead to several predictions about female group size based upon ecological constraints, total group output, and average r within groups (e.g., REEVE and EMLEN, 2000). While the inferences made here appear relatively straightforward, factors influencing reproductive skew may be complex and may interact. Thus, empirical, in particular, experimental, tests of skew theory are especially critical for the application of these models to primate behavioral ecology and evolution.

In order to evaluate each of these schemas, to assess their similar properties and predictions, and, ultimately, to test these general principles of the causes and consequences (including the genetic architecture of populations) of female group size for polygynous howlers, empirical research is required to measure the costs and benefits to females of their decisions to disperse or not to disperse and/or to tolerate or not to tolerate other females. Further investigation is also needed to measure average r within female groups, to measure patch quality, including the local abundance of resources, the degree to which resources are ephemeral and monopolizable, and the quality of resources, especially, food. Related to the assumptions of each of the schemas discussed in this paper, WITTENBERGER's (1980; also see HORWICH et al., 2001, pp. 58-59) treatment highlights the importance of measuring female survivorship and fecundity (reproductive rates) in order to assess the costs and benefits of sociality to females, a tradeoff central to each schema discussed here.

While the present discussion focuses attention upon females of polygynous howler species, it is expected to apply as well to other species for which eviction ("targeting") is characteristic. The study of female group size in mammals can be traced to early papers by GEIST (1974) and CLUTTON-BROCK and HARVEY (1976) whose ideas were influenced strongly by previous studies on territorial birds (see reviews in WITTENBERGER, 1980; WILSON, 1975). Recent models, such as the schemas discussed in this paper, are derived from those early studies, increasing the likelihood that an understanding of female group size in social mammals, indeed, in social species, is forthcoming.

References
ALTMANN, S.A.: Field observations on a howling monkey society. J. Mammal. (1959) 40: 317-330.

BOLIN, I.: Male parental behavior in black howler monkeys (*Alouatta palliata pigra*) in Belize and Guatemala. Primates (1981) 22: 349-360.

BRADBURY, J.W. and VEHRENCAMP, S.L.: Social organization and foraging in emballonurid bats III: mating systems. Behav. Ecol. Sociobiol. (1977) 2: 1-17.

BROCKETT, R.C., HORWICH, R.H. and JONES, C.B.: Female dispersal in the Belizean black howling monkey (*Alouatta pigra*). Neotropical Primates (2000) 8: 32-34.

CALEGARO-MARQUES, C. and BICCA-MARQUES, J.C.: Emigration in a black howling monkey group. Int. J. Primatol. (1996) 17: 229-238.

CANT, M.A,. and JOHNSTONE, R.A.: Power struggles, dominance testing, and reproductive skew. Amer. Natur. (2000) 155: 406-417.

CARPENTER, C.R.: A field study of the behavior and social relations of howling monkeys. Comp. Psychol. Monog. (1934) 10: 1-168.

CHAPMAN C.A. and BALCOMB, S.R.: Population characteristics of howlers: ecological conditions or group history. Int. J. Primatol. (1998) 19: 385-404.

CLARKE, M.R. and GLANDER, K.E.: Female reproductive success in a group of free-ranging howling monkeys (*Alouatta palliata*) in Costa Rica. In: SMALL, M.F. (ed.): Female Primates: Studies by Women Primatologists. New York: Alan R. Liss (1984): 111-126.

CLUTTON-BROCK, T.H.: Reproductive concessions and skew in vertebrates. TREE (1998) 13: 188-292.

CLUTTON-BROCK, T.H. and HARVEY, P.H.: Evolutionary rules and primate societies. In: BATESON, P.P.G. and HINDE, R.A. (eds.): Growing Points in Ethology. Cambridge: Cambridge University Press (1976): 195-237.

CROCKETT, C.M.: Emigration by female red howler monkeys and the case for female competition. In: SMALL, M.F. (ed.): Female Primates: Studies by Women Primatologists. New York: Alan R. Liss, Inc. (1984): 159-174.

CROCKETT, C.M.: Diet, dimorphism, and demography: perspectives from howlers to hominids. In: KINZEY, W.G. (ed.): The Evolution of Human Behavior: Primate Models. Albany: SUNY Press (1987): 115-135.

CROCKETT, C.M.: The relation between red howler monkey (*Alouatta seniculus*) troop size and population growth in two habitats. In: NORCONK, M.A., ROSENBERGER, A.L. and GARBER, P.A. (eds.): Adaptive Radiations of Neotropical Primates. New York: Plenum (1996): 489-510.

CROCKETT, C.M.: Conservation biology of the genus *Alouatta*. Int. J. Primatol. (1998) 19: 549-578.

CROCKETT, C.M. and EISENBERG, J.F.: Howlers: variations in group size and demography. In: SMUTS, B.B., CHENEY, D.L., SEYFARTH, R.M., WRANGHAM, R.W. and STRUHSAKER, T.T. (eds.): Primate Societies. Chicago: The University of Chicago Press (1987): 54-68.

CROCKETT, C.M. and JANSON, C.H.: Infanticide in red howlers: female group size, male membership and a possible link to folivory. In: van SCHAIK, C.P. and JANSON, C.H. (eds.): Infanticide by Males and Its Implications. Cambridge: Cambridge University Press (2000): 75-98.

CROCKETT, C.M. and POPE, T.: Consequences of sex differences in dispersal for juvenile red howler monkeys In: PEREIRA, M.E. and FAIRBANKS, L.A. (eds.): Juvenile Primates: Life History, Development and Behavior. New York: Oxford University Press (1993): 104-118.

DA SILVA, JR., E.C.: A preliminary survey of brown howler monkeys (*Alouatta fusca*) at the Cantareira Reserve (São Paulo, Brazil). Rev. Brasil. Biol. (1981) 41: 897-909.

DIXSON, A.F.: Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes, and Human Beings. Oxford, UK: Oxford University Press (1998).

EISENBERG, J.F.: Mammalian social organizations and the case of *Alouatta*. In: ROBINSON, M.H. and TIGER, L. (eds.): Man and Beast Revisited. Washington: Smithsonian Institution Press (1991): 127-138.

EMLEN, S.T.: An evolutionary theory of the family. Proc. Nat. Acad. Sci. USA (1995) 92: 8092-8099.

EMLEN, S.T. and ORING, L.: Ecology, sexual selection and the evolution of mating systems. Science (1977) 197: 215-223.

ESTRADA, A., CASTELLANOS, L., GARCIA, Y., FRANCO, B., MUNOZ, D., IBARRA, A., RIVERA, A., FUENTES, E. and JIMENEZ, C.: Survey of the black howler monkey, *Alouatta pigra*, population at the Mayan site of Palenque, Chiapas, Mexico. Primates (2002a) 43: 51-58.

ESTRADA, A., LEANDRA, L., VAN BELLE, S., FRENCH, K., MUNOZ, D., GARCIA, Y., CASTELLANOS, L. and MENDOZA, A.: The black howler monkey (*Alouatta pigra*) and spider monkey (*Ateles geoffroyi*) in the Mayan site of Yaxchilán, Chiapas, Mexico: a preliminary survey. Neotropical Primates (2002b) 10: 89-95.

GEIST, V.: On the relationship of social evolution and ecology in ungulates. Am. Zool. (1974) 14: 205-220.

GIUDICE, A.M.: Relaciones sociales en un grupo en cautiverio de monos aulladores negros (*Alouatta caraya*). Boletin Primatologico Latinoamericano (1993) 4:19-23.

GLANDER, K.E.: Dispersal patterns in Costa Rican mantled howling monkeys. Int. J. Primatol. (1992) 13: 415-436.

GROSS, M. R.: Alternative reproductive strategies and tactics: diversity within sexes. TREE (1996) 11: 92-97.

GROVES, C.P.: Primate Taxonomy. Washington: Smithsonian Institution Press (2001).

HAGER, R.: Reproductive skew models applied to primates. In: JONES, C.B. (ed.): Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions. Norman: American Society of Primatologists (2003): 65-101.

HORWICH, R.H., BROCKETT, R.C., JAMES, R.A. and JONES, C.B.: Population structure and group productivity of the Belizean black howling monkey (*Alouatta pigra*): implications for female socioecology. Primate Report (2001) 61: 47-65.

ISBELL, L.A. and YOUNG, T.P.: Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. Behaviour (2002) 139: 177-202.

IZAWA, K.: Social changes within a group of red howler monkeys (*Alouatta seniculus*). IV. Field Studies of New World Monkeys, La Macarena, Colombia (1992) 7: 15-27.

JOHNSON, D.D.P., KAYS, R., BLACKWELL, P.G. and MACDONALD, D.W.: Does the resource dispersion hypothesis explain group living? TREE (2002) 17: 563-570.

JOHNSON, M.L. and GAINES, M.S.: Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Ann. Rev. Ecol. Syst. (1990) 21: 449-480.

JONES, C.B.: Aspects of reproduction in the mantled howler monkey (*Alouatta palliata* Gray). Unpublished Ph.D. Dissertation, Cornell University, Ithaca, NY. (1978).

JONES, C.B.: The functions of status in the mantled howler monkey, *Alouatta palliata* Gray: intraspecific competition for group membership in a folivorous Neotropical primate. Primates (1980) 21: 389-405.

JONES, C.B.: Social organization of captive black howler monkeys (*Alouatta caraya*): "social competition" and the use of non-damaging behavior. Primates (1983) 24: 25-39.

JONES, C.B.: Reproductive patterns in mantled howler monkeys: estrus, mate choice and copulation. Primates (1985) 26: 130-142.

JONES, C.B.: Howler subgroups as homeostatic mechanisms in disturbed habitats. Neotropical Primates (1995a) 3: 7-9.

JONES, C.B.: Howler monkeys appear to be preadapted to cope with habitat fragmentation. Endangered Species UPDATE (1995b) 12: 9-10.

JONES, C.B.: Dispersal in mantled howler monkeys: a threshold model. Mastozoologia Neotropical (1995c) 2: 207-211.

JONES, C.B.: Predictability of plant food resources for mantled howler monkeys at Hacienda La Pacifica, Costa Rica: Glander's dissertation revisited. Neotropical Primates (1996) 4: 147-149.

JONES, C.B.: *Alouatta palliata* politics: empirical and theoretical aspects of power. Primate Report (2000) 56: 3-21.

JONES, C.B. and CORTES-ORTIZ, L.: Facultative polyandry in the howling monkey (*Alouatta palliata*): Carpenter was correct. Boletin Primatologico Latinoamericano (1998) 7: 1-7.

KINZEY, W.G. and CUNNINGHAM, E.P.: Variability in Platyrrhine social organization. Am. J. Primatol. (1994) 34: 185-198.

KOENIG, W.D. and HAYDOCK, J.: Dividing up the kids. Science (2001) 291: 442-443.

LOPEZ, G.S. and RUMIZ, D.: Los primates de la reserva Río Bravo, Belice. La Ciencia y el Hombre (1995) 20: 49-64.

MENDES, S.L.: Estudio ecológico de *Alouatta fusca* (Primates: Cebidae) na Estação Biológica de Caratinga, MG. Rev. Nordestina Biol. (1989) 6: 71-104.

OSTRO, L.E.T., SILVER, S.C., KOONTZ, F.W., YOUNG, T.P. and HORWICH, R.H.: Ranging behavior of translocated and established groups of black howler monkeys *Alouatta pigra* in Belize, Central America. Biol. Cons. (1999) 87: 181-190.

OSTRO, L.E.T., SILVER, S.C., KOONTZ, F.W., HORWICH, R.H. and BROCKETT, R.: Shifts in social structure of black howler (*Alouatta pigra*) groups associated with

natural and experimental variation in population density. Int. J. Primatol. (2001) 22: 733-748.

PARKER, G.A.: Assessment strategy and the evolution of fighting behaviour. J. Theor. Biol. (1974) 47: 223-243.

PEREZ-TOME, J.M. and TORO, M.A.: Competition of similar and non-similar genotypes. Science (1982) 299: 153-154.

POPE, T.R.: The influence of dispersal patterns and mating system on genetic differentiation within and between populations of the red howler monkey (*Alouatta seniculus*). Evolution (1992) 46: 1112-1128.

PULLIAM, H.R. and CARACO, T.: Living in groups: Is there an optimal group size? In: KREBS, J.R. and DAVIES, N.B. (eds.): Behavioural Ecology: An Evolutionary Approach. Sunderland: Sinauer Associates, Inc. (1984): 122-147.

PUSEY, A.E. and PACKER, C.: Dispersal and philopatry. In: SMUTS, B.B., CHENEY, D.L., SEYFARTH, R.M., WRANGHAM, R.W. and STRUHSAKER, T.T. (eds.): Primate Societies. Chicago: The University of Chicago Press (1987): 250-266.

REEVE, H.K. and EMLEN, S.T.: Reproductive skew and group size: an *N*-person staying incentive model. Behav. Ecol. (2000) 11: 640-647.

REEVE, H.K. and RATNIEKS, F.L.W.: Queen-queen conflict in polygynous societies: mutual tolerance and reproductive skew. In: KELLER, L. (ed.): Queen Number and Sociality in Insects. Oxford: Oxford University Press (1993): 45-85.

RUDRAN, R.: The demography and social mobility of a red howler (*Alouatta seniculus*) population in Venezuela. In: EISENBERG, J.F. (ed.): Vertebrate Ecology in the Northern Neotropics. Washington: Smithsonian Institution Press (1979): 107-126.

RUMIZ, D.I.: *Alouatta caraya*: population density and demography in Northern Argentina. Am. J. Primatol. (1990) 21: 279-294.

RYLANDS, A.B., SCHNEIDER, H., LANGGUTH, A., MITTERMEIER, R.A., GROVES, C.P. and RODRIGUEZ-LUNA, E.: An assessment of the diversity of New World primates. Neotropical Primates (2000) 8: 61-93.

SCHOENER, T.W.: Theory of feeding strategies. Ann. Rev. Ecol. Syst. (1971) 2: 369-404.

SEKULIC, R.: Daily and seasonal patterns of roaring and spacing in four red howler *Alouatta seniculus* troops. Folia Primatol. (1982) 39: 22-48.

SILK, J.B.: The evolution of social conflict among female primates. In: MASON, W.A. and MENDOZA, S.P. (eds.): Primate Social Conflict. Albany: SUNY Press (1993): 49-84.

SILVEIRA, R.M.M. and CODENOTTI, T.L.: Interações sociais e dieta do Bugio-Ruivo, *Alouatta guariba clamitans*, no Parque Estadual de Itapuã, Pio Grande do Sul, Brasil. Neotropical Primates (2001) 9: 15-19.

STERCK, E.H.M., WATTS, D.P. and VAN SCHAIK, C.P.: The evolution of female social relationships in nonhuman primates. Behav. Ecol. Sociobiol. (1997) 41: 291-309.

STRIER, K.B.: Reproductive ecology of New World Monkeys. In: ELLISON, P.T. (ed.): Reproductive Ecology and Human Evolution. New York: Aldine de Gruyter (2001): 351-367.

THORINGTON, JR., R.W., RUIZ, J.C. and EISENBERG, J.F.: A study of a black howling monkey (*Alouatta caraya*) population in Northern Argentina. Am. J. Primatol. (1984) 6: 357-366.

TRIVERS, R.L.: Parental investment and sexual selection. In: CAMPBELL, B. (ed.): Sexual Selection and the Descent of Man 1871-1971. Chicago: Aldine (1972): 136-179.

WEST, S.A., PEN, I. and GRIFFIN, A.S.: Cooperation and competition between relatives. Science (2002) 296: 72-75.

WEST-EBERHARD, M.J.: Sexual selection, social competition, and evolution. Proc. Am. Phil. Soc. (1979) 123: 222-234.

WILSON, E.O.: Sociobiology: The New Synthesis. Cambridge, MA: Harvard University Press (1975).

WITTENBERGER, J.F.: Group size and polygamy in social mammals. Amer. Natur. (1980) 115: 197-222.

WRANGHAM, R.W.: An ecological model of female-bonded primate groups. Behaviour (1980) 75: 262-299.

ZUCKER, E.L. and CLARKE, M.R.: Agonistic and affiliative relationships of adult female howlers (*Alouatta palliata*) in Costa Rica over a 4-year period. Int. J. Primatol. (1998) 19: 433-450.

ZUNINO, G.E., GONZALEZ, V., KOWALEWSKI, M.M. and BRAVO, S.P.: *Alouatta caraya*. Relations among habitat, density and social organization. Primate Report (2001) 61: 37-46.

Correspondence to:
Dr. Clara B. Jones, Livingstone College, School of Liberal Arts, 701 W. Monroe Street, Salisbury, NC 28144, U.S.A.; E-mail: cjones@livingstone.edu; howler425@cs.com.

MALE DISPERSAL AND PHILOPATRY IN THE AWASH BABOON HYBRID ZONE. PHILLIPS-CONROY, J.E. AND JOLLY, C.J.

Key words: baboon hybrid zone, hamadryas, anubis, dispersal regimes, biological correlates

Abstract

Nearly all male anubis baboons disperse from their natal troop, while hamadryas males are usually philopatric. This contrast is correlated with differences in trajectories of testicular and body-mass growth, and the eruption of permanent canine teeth. Hamadryas males exhibit precocious testicular growth that slows in late subadulthood, while anubis undergo a growth spurt in testicular and body size around the time of peak natal dispersal. In the contact zone between them in the Awash National Park, Ethiopia, most anubis and hamadryas exhibit taxon-typical dispersal behavior, but some adult and juvenile hamadryas males join anubis groups, probably attracted by the presence of unattached females. Members of a hybrid troop exhibit low rates of dispersal and a developmental profile with elements of both parental forms.

Introduction

Change of residence from birthplace to a potential breeding site (natal dispersal) and from one breeding site to another (breeding dispersal) has been identified as a major determinant of population genetic structure, and hence an important contribution to the evolutionary trajectory of populations and species. Among papionin monkeys (Tribe Papionini) – baboons (*Papio*), mandrills (*Mandrillus*), macaques (*Macaca*) and mangabeys (*Cercocebus* and *Lophocebus*) – as in other group-living mammals, the crucial element of dispersal is not so much geographic as social – a shifting of affiliation from one breeding group to another, which usually, but incidentally, entails a change in location. A widely accepted typology classifies residence and dispersal patterns in catarrhine primates dichotomously as female-philopatric, male dispersing (FPMD) or male-philopatric, female dispersing (MPFD). Most papionin species are FPMD, and it is reasonable to suppose that this is the ancestral condition for the taxon. In such societies, the most obvious and coherent social unit is a bisexual troop, often with more than one resident, adult male, and discernible, ranked, matrilineages of females and young. Males normally emigrate from their natal troop, and join another, before breeding, so that all animals normally have one natal and one immigrant parent, and the effective population size is much larger than the social group.

Within the genus *Papio*, the so-called savanna baboons (that is, all extant forms of *Papio* apart from the hamadryas, which are often grouped into a single species, *P. cynocephalus*), exhibit some form of FPMD pattern. There is, however, much variation among taxa, populations and individuals in the incidence, timing, and demographic correlates of inter-group migration. An assumption implict in most reviews of baboon dispersal (and other) behavior is that whereas the difference between

hamadryas and savanna baboons is taxon-specific and presumably genetically based, populational and individual variation among savanna baboon populations is best explained in terms of the immediate impact of environmental and societal cues upon a uniform, shared but individually plastic dispersal phenotype. This assumption is not necessarily valid, however, since the savanna baboons are not a monophyletic sister group of hamadryas. There is thus no *a priori* reason to assume that the behavioral differences among them, though they may be less striking than those distinguishing the hamadryas, are any less genetically determined. Anecdotal (STRUM, 1987; SAPOLSKY, 1986, 2001) and quantitative (PACKER, 1979; ALBERTS and ALTMANN, 1995, 2001) accounts suggest that anubis baboons, at least in East Africa, are distinguished by undergoing natal dispersal more consistently, and more often, as juveniles than, for example, yellow baboons. Suspecting that the "savanna baboon" rubric may conceal more population-specific behavioral polytypy than is widely assumed, we do not attempt here to summarize the dispersal behavior of all non-hamadryas baboons, confining comparisons to anubis and hamadryas.

Female anubis baboons are strongly philopatric, and the most enduring intra-troop social structures are lineages of related females (SMUTS, 1985). Male dispersal before breeding is the norm, and a male may make multiple subsequent migrations, including reverse migration, to a group where it previously resided. Though both earlier and later migration have been documented, a male typically leaves his natal group in young adulthood, at 100-120 months, and moves to a neighboring group (PACKER, 1979; PUSEY and PACKER, 1986). Two distinct forms of relationship between an (immigrant) adult male and resident females, if successfully developed, enhance different aspects of male reproductive success. Mating success, for a young, newly-arrived male, in particular, depends upon consortships established and defended during the female's periovulatory period. A consorting male attempts to exclude rivals by direct threat and, sometimes, physical combat, and by closely following and guarding the female. In spite of these attempts, however, mating is usually polyandrous in multi-male troops, as one male supplants another. In the other mode of social interaction – "friendship" – a male, especially in older age, may defend his reproductive investment in infants already sired, and also may attain, by hedonic ingratiation, some matings that he could no longer win agonistically.

The hamadryas baboon (*Papio hamadryas*) is often described as a MPFD species. The latter designation, however, fails to convey the mechanics of dispersal in the complex hamadryas social organization, which has been aptly described as multi-leveled (KUMMER, 1968a,b; KUMMER, 1988, 1995). The hamadryas social unit homologous to the troop of FPMD societies is known as a band. Juvenile male hamadryas have been reported to make temporary excursions into neighboring bands, but in all observed cases returned to their own (SIGG et al., 1982; ABEGGLEN, 1984). Maturing in their natal band, males form loose associations (clans) with male relatives.

The male-female relationships that in anubis baboons are divided between "mates" and "friends" are combined in hamadryas society. Both mating and hedonic, grooming-based, male-female interactions are confined quasi-exclusively within highly coherent, male-led one-male units (OMUs). As the OMU is the locus of almost all female social interactions, there is no pervasive matrilineal organization within

the band, and OMUs of a band often follow independent paths when foraging. Juvenile females are recruited from their natal OMU to form the nucleus of the new OMU of a "bachelor" band member. Such females might be described as "dispersing" from their natal OMU, but the movement involved is minimal, since their future mate is almost certainly born in the same band, and, probably, in the same clan. As the leader male of an OMU loses control of it with age or incapacity, the females will be immediately recruited by another male, perhaps from a different clan or even a neighboring band. The resultant, sporadic movement of females, which presumably may occur at any time in their reproductive career, may have far-reaching, long-term population-genetic consequences (HAPKE et al., 2001) but is surely distinct in motivation and effects from the male dispersal seen in FPMD species.

The hamadryas OMU-based social system is associated with physical as well as behavioral autapomorphies. These include more obvious sexual dimorphism in adult pelage, with the male's luxuriant mane probably functioning as an organ of attraction to females (JOLLY, 1963; KUMMER, 1968a,b, 1988) as well as an honest signal of his condition (ZAHAVI, 1975) to both mates and potential rivals. In association with low rates of sperm competition in hamadryas, adult testis size is both absolutely and relatively smaller than in, for instance, anubis baboons (JOLLY and PHILLIPS-CONROY, 2003). In juvenile life, however, testicular development is somewhat accelerated in hamadryas compared to anubis, perhaps because young hamadryas, maturing in their natal group, are able to initiate the taxon-specific "follower strategy" that can lead ultimately to OMU leader status. By contrast, male anubis (and presumably other "savanna" baboons with male dispersal) have to delay serious reproductive activity until they are established (among potentially hostile non-kin) in their adopted troop. A spurt in body-mass growth, not seen in hamadryas, occurs immediately before the usual age of dispersal and results in an absolutely larger adult body mass. In the present paper, we examine developmental trajectories of other features that might be expected to co-vary with male philopatry or dispersal: the circumferences of proximal limb segments and thorax (largely a correlate of muscularity) and the eruption of the permanent canine teeth.

Although they exemplify contrasting regimes of social behavior and sex-specific dispersal, with associated physical and developmental characteristics, hamadryas are sufficiently close genetically to olive baboons that they can and do interbreed in nature, forming viable and fertile hybrids in narrow hybrid zones, including one situated in the Awash National Park (ANP), Ethiopia, where the data for this paper were gathered. Such zones of contact and hybridization are likely to be of relevance in understanding both the proximate underpinnings and ultimate evolutionary causation of inter-taxon differences, including differences in the causes and correlates of dispersal. First, they provide a common arena in which the taxon-specific programs of the two taxa are carried out under ecological conditions that, if not uniform, are less divergent than would be the case for more central populations. For example, though most hamadryas baboons live in semi-desert habitats, while anubis are found in more mesic habitats over most of their range, in the ANP both live in a habitat dominated by *Acacia* bush, with patches of more productive habitat consisting of riverine forest or groves of doum palm (*Hyphaene thebaica*). To the extent that dispersal behavior is determined plastically by the immediate ecological situation, patterns exhibited by the two taxa should tend to converge in the boundary zone. Sec-

ond, the habitat of the contact zone is literally marginal for both taxa, and therefore likely to test the limits of plasticity in their species-specific, ecologically adaptive programs. The habitat is also subject to fluctuations in quality over time, driven by unpredictable annual rainfall. Years with high annual rainfall and high vegetational productivity should favor the coherent foraging groups of anubis, and thus make the habitat less favorable to hamadryas, and vice versa. Models (HANSKI et al., 2001) predict that in such temporally fluctuating habitats, a tendency to disperse (whether plastic or genetic) should be enhanced. Third, contact zones allow direct social interaction between individuals with different, taxon-specific behavioral programs, which again tends to stimulate behaviors unlikely to be observed in more central populations. Finally, in the hybrids themselves taxon-specific gene complexes are dismantled and recombined, potentially throwing light on the heritable component of developmental and behavioral programs.

In the present paper we use observational, trap-retrap, physiological, genetic, and morphometric data from the ANP populations of olive and hamadryas baboons, and their natural hybrids, to investigate some correlates of male dispersal and philopatry. Direct observations and capture data document the occurrence of migration and, in a few cases, the age at which it occurred, and some additional inferences about migration are drawn from the distribution of mitochondrial haplotypes (NEWMAN, 1997) and microsatellite markers (WOOLLEY-BARKER, 1999). The morphometric data allow us to explore the biological characteristics of males as they mature and to compare the taxa in features that relate to male competition. Our data are thus more heterogeneous than those drawn from continuous observation of a few, neighboring, social groups (e.g., ALBERTS and ALTMANN, 1995, 2001). On the other hand, by including groups over a 60km span, we are able to document some long-range dispersal events, notoriously under-represented in most studies of large, comparatively vagile vertebrates.

Materials and Methods

The ANP study population (NAGEL, 1973; PHILLIPS-CONROY, 1978; PHILLIPS-CONROY and JOLLY, 1981, 1986, 1988; PHILLIPS-CONROY et al., 1986, 1991, 1992) consists of olive, hamadryas, and hybrid baboon groups. The area and its baboons were first documented in the late 1960's (KUMMER, 1968a,b, 1988, 1995; NAGEL, 1973) . Several groups were investigated by Shotake and his colleagues in the mid-1970s (SHOTAKE et al., 1977, 1981; SUGAWARA, 1982), and a group from Bristol University carried out a short behavioral study of Awash anubis baboons (ALDRICH-BLAKE et al., 1971). In 1972-73, and from 1982 to the present, the Awash baboons have been investigated by the Awash National Park Baboon Research Project, or ANPBRP (JOLLY and BRETT, 1973; BRETT et al., 1977, 1982; PHILLIPS-CONROY and JOLLY, 1981, 1986, 1988; PHILLIPS-CONROY et al., 1986, 1991, 1992; JOLLY, 1993; JOLLY and PHILLIPS-CONROY, 2003).

The central objective of the ANPBRP was, and is, to investigate the structure and dynamics of the hybrid zone by mapping across it the distribution of phenotypic variation and discrete genetic markers. Most data for this purpose have been collected by live capture, sampling, marking, and release, from 11 baboon groups (Groups A – K) whose linear distribution along the Awash River transects the hybrid zone (Fig-

ure 1). Over 10 months of 1973, 534 animals from these groups were trapped and sampled by F.L. Brett and R.G. Cauble (BRETT et al., 1982). In 1982 – 2000, we carried out 14 trapping seasons of 1-2 months duration (in 1982, 1983, 1984, 1986 (twice), 1988, 1989, 1990, 1991, 1993, 1995, 1997, 1998, and 2000), concentrating on two or three of the anubis (B-F) or hybrid (G-J) groups each season. Hamadryas groups A and K have not been accessible since the 1972-73 season, but in 1997 we investigated hamadryas groups living in the northern end of the ANP, at the site of Filwoha (see also SWEDELL, 2000).
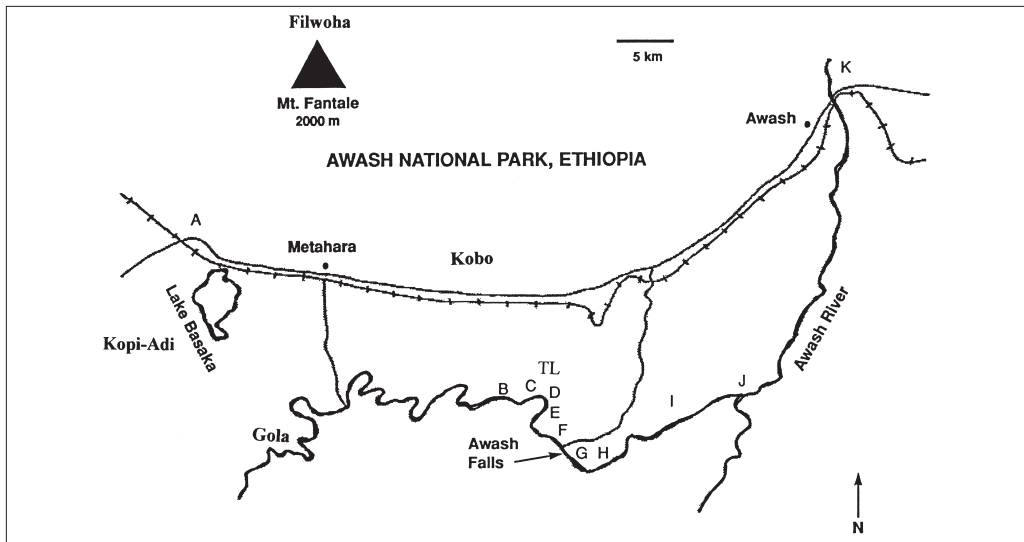

Fig. 1: Map of Awash National Park and placement of baboon groups studied by the Awash National Park Research Project.

The ANPBRP's scope has widened over time to include the documentation of physiological and developmental divergences between the two parental populations, and social behavior in "pure," mixed, and hybrid social groups. Observational studies, averaging 18 months duration, were carried out on Groups C (NYSTROM, 1992), D (BEYENE, 1998), H (BERGMAN, 2000; BEEHNER, in prep.) and Filwoha (SWEDELL, 2000). In the course of his study, Beyene was able to add additional information derived from phenotypically mixed groups living at the site of Gola, from an anubis group (TL) whose range overlapped those of Groups D and C, and from a hamadryas group, Kobo, living on the southern slopes of Mt. Fantale (Figure 1).

Methods of capture and sedation are described elsewhere. (BRETT et al., 1982 ; PHILLIPS-CONROY et al., 1991, 1992; JOLLY and PHILLIPS-CONROY, 2003). In all seasons, including 1973, the sedated animal was assessed for age (by dental eruption; PHILLIPS-CONROY and JOLLY, 1988), sex and hybridity (from external phenotype; NAGEL, 1973; PHILLIPS-CONROY, 1978; PHILLIPS-CONROY and JOLLY, 1986), then weighed and photographed, its body length measured, its upper left dental quadrant cast, its palmar dermatoglyphics recorded, and a sample of hair and blood collected. From 1983 on, animals were ear tagged and we collected addi-

tional morphometric data, including lengths of limb segments, circumferences of trunk and limbs, and testicular dimensions. In 1995, 1997, 1998 and 2000 cerebrospinal fluid of selected animals was sampled by cisternal puncture (KAPLAN, 1999 a,b) and later assayed for metabolites of three neurotransmitters.

Dental eruption status was assessed by visual inspection, and each tooth was rated as either never erupted, erupting, or fully erupted, and the age of immature animals estimated from an established eruption chronology (REED, 1973; PHILLIPS-CONROY and JOLLY, 1988). Animals caught as juveniles were aged when retrapped as adults by adding their estimated age at first capture to the interval between captures. When arranged in order of increasing occlusal wear on their molars, these animals comprised a reference set used to estimate the age of animals first caught as adults (PHILLIPS-CONROY et al., 2000). For some analyses, animals were broken into five age classes: 1: Infant: No permanent molars visible (< 24 months); 2: Younger juvenile: One or more first molars visible, no M2s (24-50 months); 3: Older Juvenile: One or more second molars visible, no M3s (50-80 months); 4: Subadult: One or more third molars visible, but dental eruption not complete (80-100 months); 5: Full adult: Dentition (including canines) completely erupted (> 100 months).

Body mass was measured on a spring scale, and somatic dimensions were taken with a cloth tape. Data collected in all field seasons are used in the analysis, with the following exceptions: we exclude body weight data from the famine year of 1973, when animals were approximately 10 % lighter than in following years of normal rainfall, and somatometric data collected in 1993, some of which are suspected of being anomalous. In regression analyses, we use (estimated) age in months as the independent variable; in other analyses we use age class. Preliminary examination showed that the size and robusticity measures plateaued and, in some cases, tended to decline after about 120 months (estimated) age, which is also the age at which other studies on these animals have found most natal migration to be complete (PUSEY and PACKER, 1986). Animals older than this were therefore excluded from calculations of growth rates and comparisons across taxa.

Table 1 presents the means, standard deviations and sample size for each variable by age class within hamadryas, anubis, and hybrids. The column headed "%ADULT" expresses each mean value as a percentage of the mean for adult males of 120 months or less. In all cases the comparisons were done using non-parametric statistical tests; for pairwise comparisons, the Mann-Whitney test was used, while, for three-way comparisons, we used the Kruskal-Wallis test. Comparisons between adjacent age classes for each of the three groups (anubis, hamadryas and hybrids) are presented in Table 2, while Table 3 compares anubis, hamadryas and hybrid males males of the same age class.with each other.

The morphometric data are graphically presented in Figures 2-9. We plotted each measure of body size and limb robusticity against estimated age in months (the relationships are shown as LOWESS curves in Figures 2-7) and then calculated the residuals from the corresponding linear regressions. In Figure 8 the residuals are plotted by age class. In order to examine incremental growth against a finer scale, we also plotted average growth of each variable for two year age intervals (Figure 9 A-G), and, for weight and testis size, we calculated average daily growth per two-year period in each taxon (Figure 9 B and D). We examined the relative timing

Table 1: Morphometric data for anubis, hamadryas and hybrid baboon males.

	Age-class	ANUBIS				HYBRID				HAMADRYAS				
		MEAN	SD	N	%ADULT	MEAN	SD	N	%ADULT	MEAN	SD	N	%ADULT	Sig.
Weight	1	2.73	1.11	23	12.4	2.56	0.78	11	13.3	3.74	0.30	4	17.9	NS
	2	6.11	1.47	102	27.7	4.85	1.28	16	25.3	5.77	1.49	11	27.6	0.01
	3	12.41	3.17	116	56.2	11.27	3.09	14	58.7	12.48	2.79	15	59.7	NS
	4	17.52	2.32	36	79.4	15.16	2.18	3	79.0	17.72	3.15	11	84.8	NS
	5	22.07	2.06	94	100.0	19.19	3.64	9	100.0	20.89	1.71	13	100.0	0.01
Testis	1			0	0.0			0	0.0			0	0.0	
	2	1.02	1.09	27	2.2	0.52		1	1.2	1.25	0.64	6	4.7	NS
	3	14.11	11.90	85	30.2	12.69	8.56	11	28.7	14.36	7.77	15	53.6	NS
	4	33.36	12.20	31	71.5	24.95	12.90	3	56.5	26.00	7.06	11	97.1	NS
	5	46.69	13.06	79	100.0	44.15	14.17	8	100.0	26.77	4.46	13	100.0	<.001
Relative Testis Size	1			0	0.0			0	0.0			0	0.0	
	2	0.15	0.15	27	7.1	0.09	.	1	3.8	0.20	0.09	6	15.5	NS
	3	0.98	0.73	85	46.7	1.12	0.70	11	47.1	1.11	0.53	15	86.1	NS
	4	1.88	0.58	31	89.5	1.59	0.72	3	66.8	1.47	0.30	11	114.0	NS
	5	2.10	0.55	79	100.0	2.38	0.57	8	100.0	1.29	0.24	13	100.0	<.001
Maximum Girth	1	28.10	3.85	23	44.6	27.58	2.49	6	45.6	31.83	0.60	4	50.8	NS
	2	38.25	3.30	83	60.7	35.11	3.02	15	58.0	37.70	2.85	10	60.2	0.01
	3	49.64	5.01	95	78.8	47.91	4.21	12	79.2	49.69	5.30	15	74.5	NS
	4	57.46	3.27	33	91.2	52.03	4.38	3	86.0	57.53	3.49	11	91.8	NS
	5	63.00	3.00	80	100.0	60.51	4.82	8	100.0	62.66	2.92	13	100.0	NS
Arm Circum-ference	1	10.06	1.78	24	41.4	10.37	0.67	6	45.5	12.38	0.94	4	51.0	0.03
	2	14.24	1.71	83	58.6	13.34	1.44	15	58.4	14.64	1.50	10	60.3	NS
	3	18.89	2.43	95	77.8	17.99	2.24	12	78.9	19.41	1.87	15	79.9	NS
	4	21.26	1.57	34	87.5	20.27	1.10	3	88.9	22.88	3.04	11	94.2	0.02
	5	24.29	2.03	81	100.0	22.81	2.21	8	100.0	24.30	1.55	13	100.0	NS
Thigh Cirum-ference	1	13.63	2.90	24	39.9	13.67	1.38	6	43.6	17.15	1.36	4	50.4	0.03
	2	20.18	2.52	82	59.1	18.82	1.80	15	60.1	20.45	1.85	10	60.1	NS
	3	26.98	3.56	96	79.1	25.82	2.31	12	82.4	26.79	1.32	15	78.7	NS
	4	29.67	2.98	34	86.9	27.53	3.06	3	87.8	31.06	3.56	11	91.2	NS
	5	34.13	2.95	81	100.0	31.34	2.23	8	100.0	34.04	1.50	13	100.0	0.02

of canine to molar eruption in anubis, hamadryas, and hybrid males. Each of the four canines is separately classed as: Never erupted (1), Erupting (2), or Fully erupted (3). The scores for the four teeth are then averaged. Figure 10 shows canine eruption scores for each of the age classes, which are, of course, themselves based upon molar eruption. The bars indicate the mean for taxa, with 95 % confidence intervals.

Some information about migration was drawn from surveys carried out during trapping seasons and gathered during the course of the observational studies by Nystrom, Beyene, Swedell, Bergman, and Beehner. During trapping seasons, only a few distinctive animals could be recognized individually, but these included some obvious immigrants such as hamadryas males in anubis groups. In the extended studies, observers could individually recognize most individals in the anubis or hybrid group they were studying, including all adult males and most adult females. Nystrom (NYSTROM, 1992) observed Group C, an 80-90 member anubis troop, for 13 months, and Beyene (BEYENE, 1998) conducted a 14 month study of Group D, an anubis group with approximately 90 members, of which 14 were adult males. Bergman's (BERGMAN, 2000) and Beehner's (BEEHNER, 2003, in prep.) consecutive studies yielded 28 months of observation of Group H, with 9 hybrid, 5 anubis, and 2 hamadryas males. Observers recorded the first appearance and disappearance of recognizable animals, and these data are used to estimate migration rates.

The methods used to extract genetic data have been described elsewhere (NEWMAN, 1977; WOOLLEY-BARKER, 1999).

Table 2 : Tests for significant differences between adjacent age classes within each taxon (all pairwise comparisons were done using the Mann-Whitney test).

	Classes	ANUBIS		HYBRID		HAMADRYAS	
		Abs.diff	Sig	Abs.diff	Sig	Abs.diff	Sig
Weight	1-2	3.38	<.001	2.29	<.001	2.03	<.001
	2-3	6.03	<.001	6.42	<.001	6.71	<.001
	3-4	5.11	<.001	3.89	NS	5.24	<.001
	4-5	4.55	<.001	4.03	NS	3.17	.006
Testis volume	1-2	ND	ND	ND	ND	ND	ND
	2-3	13.09	.006	12.17	NS	13.11	<.001
	3-4	19.25	<.001	12.26	.06	11.64	<.001
	4-5	13.33	<.001	19.20	NS	.77	NS
Relative testis size	1-2	ND	ND	ND	ND	ND	ND
	2-3	.83	<.001	1.03	NS	.91	<.001
	3-4	.90	<.001	0.47	NS	.36	.027
	4-5	.22	<.001	0.79	NS	-.18	NS
Maximum girth	1-2	10.15	<.001	7.53	<.001	5.87	.002
	2-3	11.39	<.001	12.80	<.001	11.99	<.001
	3-4	7.82	<.001	4.12	NS	7.84	<.001
	4-5	5.54	<.001	8.48	<.001	5.13	.001

	Classes	ANUBIS		HYBRID		HAMADRYAS	
		Abs.diff	Sig	Abs.diff	Sig	Abs.diff	Sig
Arm circum-ference	1-2	4.18	<.001	2.97	<.001	2.26	.014
	2-3	4.65	<.001	4.65	<.001	4.77	<.001
	3-4	2.37	<.001	2.28	.07	3.47	.002
	4-5	3.03	<.001	2.54	NS	1.42	NS
Thigh cir-cumference	1-2	6.55	<.001	5.15	<.001	4.30	.008
	2-3	6.80	<.001	7.00	<.001	6.34	<.001
	3-4	2.69	<.001	1.71	<.001	4.27	<.001
	4-5	4.46	<.001	3.81	NS	2.98	.011

Table 3: Comparison of anubis, hamadryas, and hybrid males within each age class. If statistical difference was found, pairwise comparisons were performed using Mann-Whitney U tests.

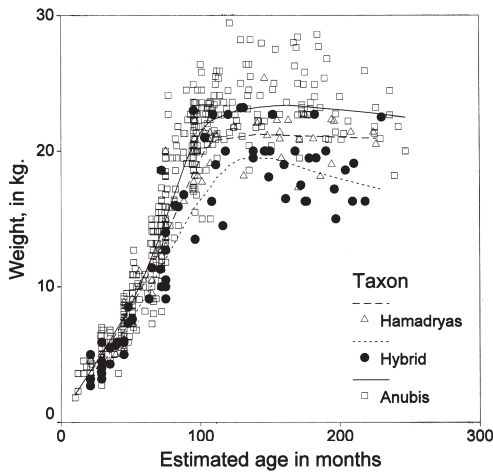|	Ageclass 2	Ageclass 3	Ageclass 4	Ageclass 5
Weight				
Kruskal-Wallis	NS	.053	NS	.000
AN-HA		NS		.006
AN-HY		.020		.001
HA-HY		NS		.051
Testis volume				
Kruskal-Wallis	NS	NS	NS	.000
AN-HA				.001
AN-HY				.056
HA-HY				.001
Relative testis size				
Kruskal-Wallis	NS	NS	NS	.000
AN-HA				.000
AN-HY				NS
HA-HY				.001
Maximum girth				
Kruskal-Wallis	.010	NS	NS	.002
AN-HA	NS			NS
AN-HY	.003			.001
HA-HY	.070			.025

Fig. 2: Bivariate plot: body weight (in kilograms) against age.
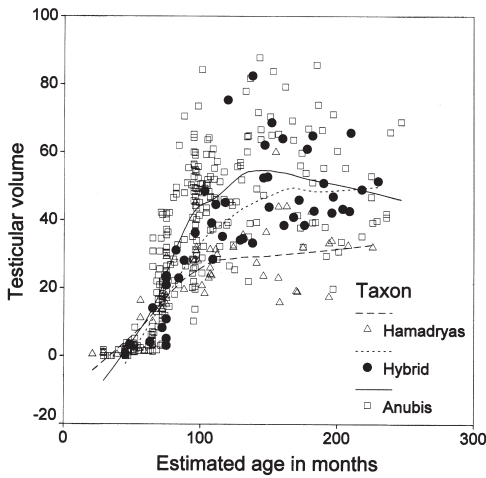

Fig. 3: Bivariate plot: testis volume (cc) against age.
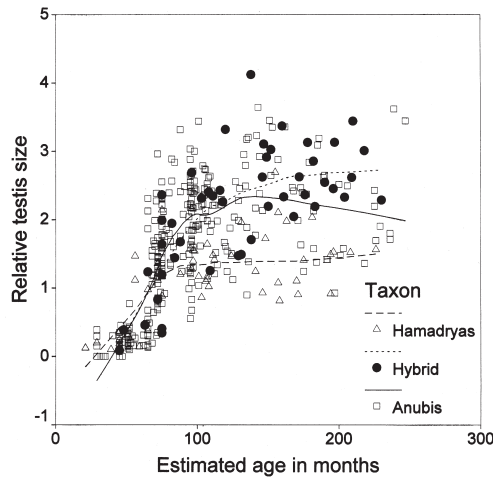

Fig. 4: Bivariate plot: relative testis size against age.
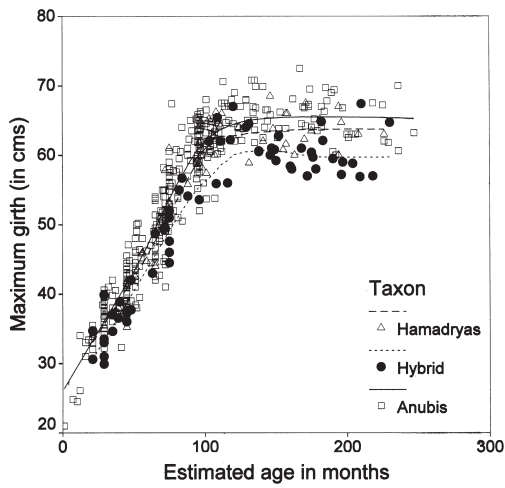
Fig. 5: Bivariate plot: maximum girth (cm) against age.
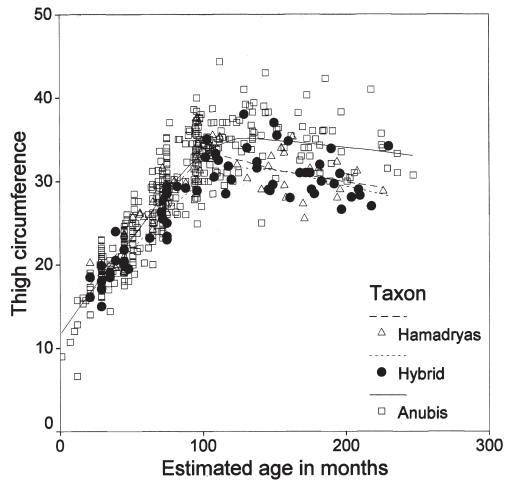

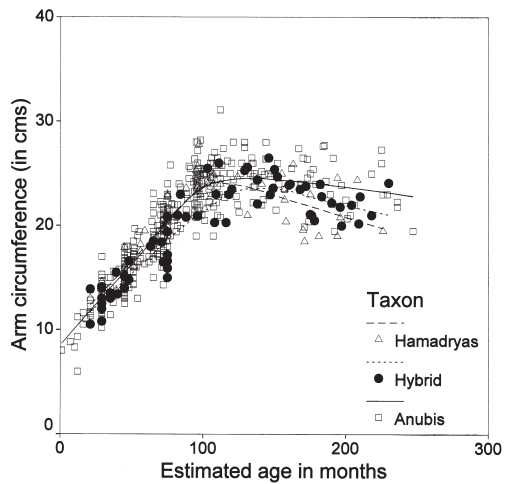Fig. 6: Bivariate plot: thigh circumference (cm) against age.

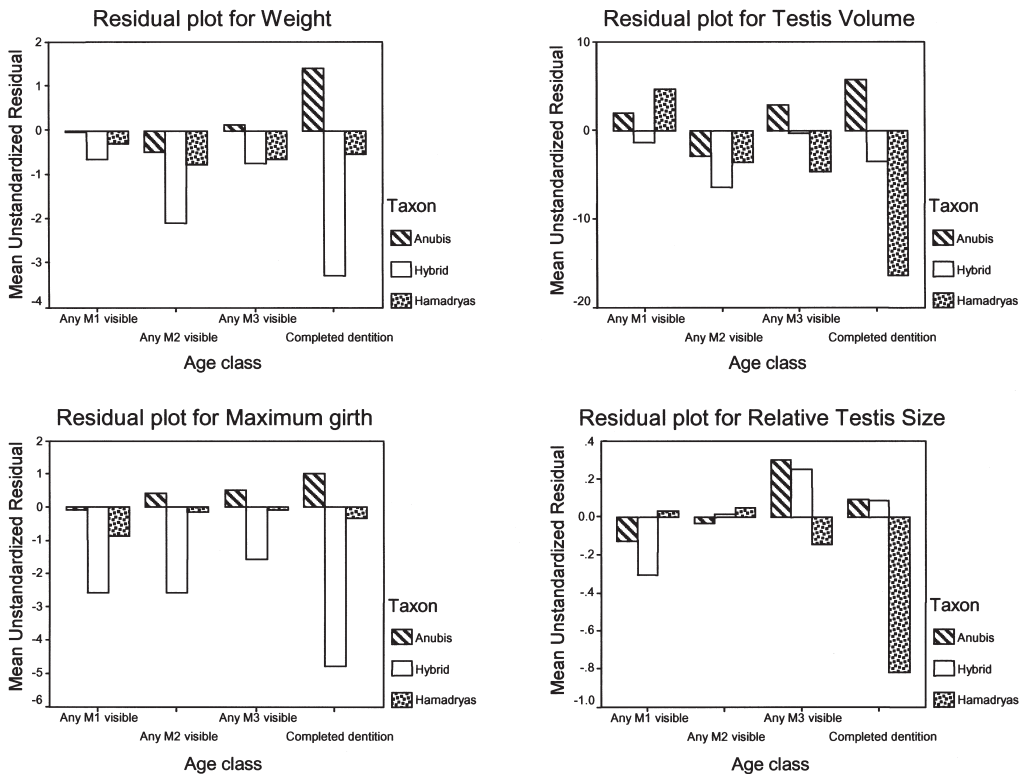Fig. 7: Bivariate plot: arm circumference (cm) against age.

Fig. 8: Plot of residuals of weight, testis size, relative testis size, and maximum girth by age class.
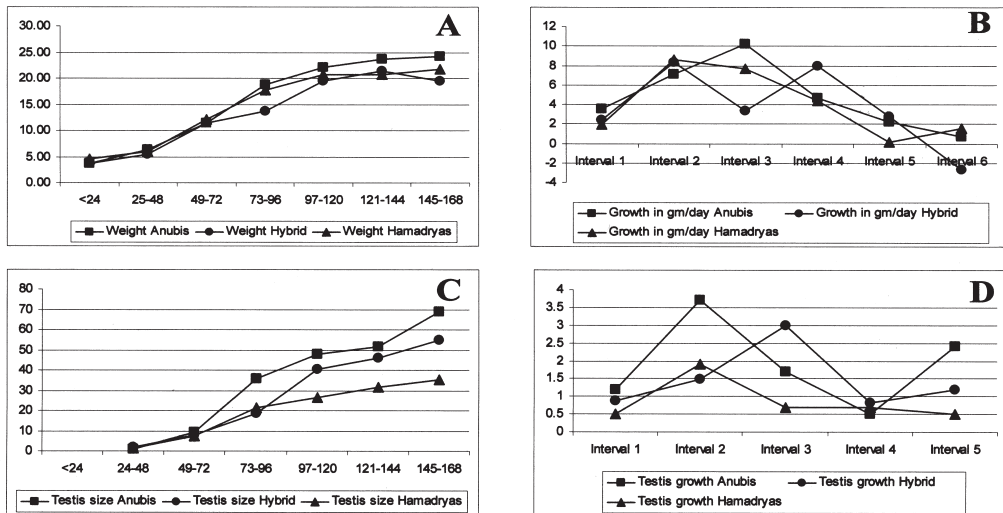

Fig. 9: Plots of morphometric data in two year intervals: A: Weight; B: Growth (g/day); C: Testis volume; D: Testis growth (cc/day).
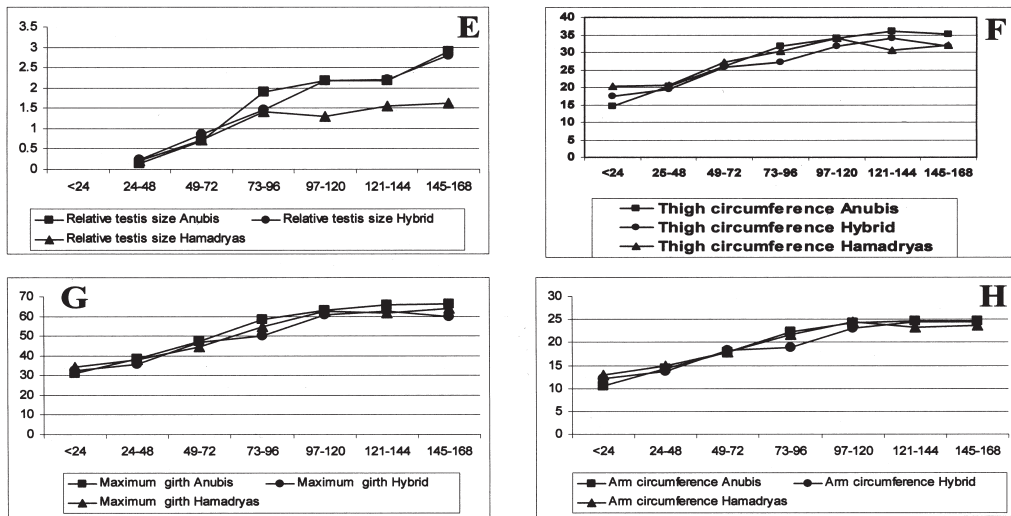
Fig. 9: Plots of morphometric data in two year intervals: E: Relative testis size; F: Thigh circumference; G: Maximum girth; H: Arm circumference

Results

Observed Migrations

The long-term studies of Groups C, D, and H documented 203, 196, and 448 adult-male-baboon-months, respectively. The immigration rate can be calculated as N_{imm} / N_{mths} , and the emigration rate as $N_{em} / (N_{mths} \times N_{adm})$, where N_{imm} is the number of observed adult male immigrants, N_{em} is the number of observed adult male emigrations, N_{adm} is the number of adult males resident in the troop, and N_{mths} is the number of months of observation. At the start of Nystrom 's (NYSTROM, 1992) study of Group C, the group included 12 adult males: 5 phenotypic anubis, 4 anubis-like hybrids, and 3 hamadryas. During the study period, 5 adult males (3 anubis-like hybrids and 2 anubis) joined the group, and one hamadryas emigrated. One of the immigrant males was estimated as approximately 8 years old, two as "middle aged", and two estimated to be "old". One immigrant was individually recognized and known to come from the neighboring Group D.

During Beyene 's (BEYENE, 1998) 14 month study, Group D included 14 adult males, 13 of which were anubis and one hamadryas. A hybrid male and an anubis male immigrated into the group during his study, and four animals (two young adults, one prime, and one old moved to adjacent groups). Three males went to TL, all within a single month. There had been three adult males in TL before the D males immigrated; after the D males immigrated, only one of the original TL males remained. The D males immediately began consorting in TL.

Bergman 's (BERGMAN, 2000) and Beehner 's (BEEHNER, 2003 in prep.) consecutive studies of Group H totaled 448 adult-male-baboon-months. This predominantly hybrid group included 11 hybrid, 5 anubis, and 2 hamadryas males. No emigration occurred, but one hamadryas-like hybrid male immigrated. Group H thus

had an immigration rate of 0.04 events/month and an emigration rate of zero. This compares with immigration rates of 0.38 and 0.143, and emigration rates of 0.005 and 0.02, respectively, for Groups C and D. This low level of migration contrasts with observations (SUGAWARA, 1988) of the same group some 20 years previously, which documented immigration and emigration rates of 0.133 and 0.032, respectively.

Cross-Migrants

If strikingly distinct from their group-mates in taxon-specific phenotypic features, individual members of an anubis or hamadryas group could be identified as migrants, even if their immigration was not documented by observation or recapture. Including both those captured and those known individually but not caught, we estimate that 25-30 adult male hamadryas migrated into the anubis zone during the years 1973-1990 (PHILLIPS-CONROY et al., 1991, 1992). While most of these were observed in only a single season, and presumably emigrated again, some recognizable individuals were long-term residents in their adopted group. Individual 10720 was first captured as an adult in Group D in 1988, and he was still resident there in 1998 but was not seen in 2000. Individual 10700 was first seen in Group F in 1982 and was resident there until his death in 1994. As described previously (PHILLIPS-CONROY et al., 1991, 1992), most, though not all, of the immigrant hamadryas captured in anubis groups had "purer" hamadryas pelage than most individuals in the closest hamadryas bands, Groups A and K, and more closely resemble hamadryas from Filwoha. We assume that these immigrants originated in more distant groups, perhaps Filwoha, or, perhaps, Kobo, where Beyene (personal communication, 1998) observed a hamdryas group meeting and mingling at a waterhole with Group D during the dry season.

Some male hamadryas evidently enter anubis groups as juveniles. A 5 year old and a 3 ½ year old hamadryas were observed, and then captured, in Group C. The older of these emigrated shortly after release, but the younger was recaptured in Group C in two subsequent seasons, the last time at the age of 8. A 2 ½ year old hamadryas male (see 10948, Table 4) was first observed in Group D early in 1993. He remained in this group until 1997 or early 1998, when he moved to Group E, where he was trapped as a young adult in July 1998.

Table 4: Cases of intertroop migration by male Awash baboons.

ID	Capture year	Age class	Age (est.)	Weight	Troop
10788	1989	2	45	8.60	C
	1991	3	70	15.50	D
10920	1991	2	47	9.50	B
	1993	3	77	22.70	C
10948	1993	2	29	4.20	D
	1998	4	88	16.30	E

ID	Capture year	Age class	Age (est.)	Weight	Troop
	1989	2	45	6.80	C
10800	1991	4	70	12.70	B
	1997	5	95	20.00	C
10818	1989	3	52	10.90	C
	1991	5	77	24.10	B
10900	1991	4	80	19.50	D
	1993	5	111	25.50	C
	1973	3	52	8.39	B
10009	1982	5	165		F
	1983	5	177	22.65	F
	1984	5	189	25.37	F
10022	1973	3	75	15.42	B
	1986	5	236	24.46	D
10377	1973	3	75	9.30	H
	1982	5	184		F
	1983	3	66	11.78	F
10610	1983	3	77	15.86	F
	1986	5	95	22.65	G
	1986	2	35	5.89	F
10673	1988	3	59	9.97	F
	1997	5	173	23.18	FILWOHA
10811	1989	3	51	8.20	B
	1997	5	152	24.55	C
	1989	2	29	6.40	C
10815	1993	5	84	21.80	D
	1998	5	144	21.80	D
10878	1990	2	45	5.50	C
	1995	5	106	23.50	D
	1988	4	80	15.86	F
10763	1989	5	93	22.70	F
	1995	5	170	25.00	G
	1990	2	45	5.90	D
10874	1993	5	83	19.50	D
	1997	5	129	23.18	C
	1983	5	140	21.74	F
10594	1986	5		20.84	D
	1988	5	141	22.20	D
	1983	5		22.65	D
10601	1986	5		21.29	F
	1988	5		21.29	F

ID	Capture year	Age class	Age (est.)	Weight	Troop
10608	1983	5	170	22.65	D
	1984	5	182	24.92	D
	1986	5	200	24.01	D
	1989	5	226	23.20	C
	1990	5	242	21.80	C
10616	1983	5	112	21.29	D
	1984	5	124	21.74	F
	1986	5	142	22.20	D
	1990	5	190	20.90	C
10952	1993	5		21.40	F
	1998	5		21.80	D
11084	1997	5	84	21.82	C
	1998	5	96	22.20	D

At least two, and probably three, anubis or anubis-like hybrid males have been observed living with one or another of the three hamadryas bands that frequent Filwoha (SWEDELL, 2002, personal communication). One of these animals (see 10673, Table 4) was caught in 1997 and identified by ear tag as a long-distance migrant then aged 14+ years. This male had been previously trapped twice in anubis Group F, as a 3-year-old in 1986, and as a 5-year old in 1988. To reach Filwoha, this animal must have traveled about 35 km in straight-line distance, crossed a major highway and several kilometers of flat, almost treeless grassland affording few baboon refuges, and bypassed several geographically intermediate baboon troops.

Recapture

One hundred eighty-three captures were retraps of male animals caught in a previous field season. One was recaptured 4 times, 9 were recaptured 3 times, 39, twice, and 134, once. Intervals between repeat captures ranged from 6 to 161 months. Of these recaptures, ten involved hamadryas living in anubis troops, and one an anubis resident in a hamadryas group, discussed in the previous section. The remaining 172 recaptures involved anubis or anubis-like hybrids, living in Groups B – H. Twenty-two of them had changed troop affiliation since their last capture (see Table 4), but since we do not have birth records for individual males, we cannot reliably distinguish natal from secondary migration. In 1973, 2/16 juvenile males from Group C carried a mitochondrial haplotype unrepresented among the females of their group (JOLLY et al., in prep.), strongly suggesting that a sizeable proportion of anubis males in the ANP, as elsewhere (STRUM, 1985; SAPOLSKY, 2001; ALBERTS and ALTMANN, 1995), may make their natal emigration well before sexual maturity.

In the present sample, three anubis males (10788, 10920, 10948) are known to have migrated at least once before full adulthood, since they were still immature (estimated at 70-80 months in age) when recaptured. Another male (10800) captured at 45, 70, and 95 months of age, moved during both intervals, from Group C to B and back again. Most of the anubis and hybrid males that had moved between trappings were recaptured in a group whose range adjoined or overlapped that of the group in

which they were previously caught. One animal (10616) trapped four times was captured in three different, contiguous groups.

As shown in Table 4, a number of anubis or anubis-like males were captured in the same troop both as a juvenile and as an adult. Since our observations were not continuous, we cannot tell in any particular case whether an animal was born in the troop and never left it, or had previously left and returned, or had immigrated as a juvenile from another troop. If the latter, some of the juvenile migrations must have occurred before the age of 4 years.

Hybrid Group H is unique in the Awash sample in that its mitochondrial diversity in 1973 suggests that its founder females were almost equally of anubis and hamadryas ancestry (NEWMAN, 1997). In earlier decades, the males of this group were not philopatric. Consistent with the movements observed in the mid to late 1970's by Sugawara (SUGAWARA, 1982, 1988), male 10377 was trapped in 1973 as 6-year old in Group H, and in 1982 as a 15-year-old in anubis Group F (Table 4). As described above, however, the male membership of Group H was very stable over 28 months of observation in 1997-2001, and retrap data also suggest that few male migrations occurred in recent years. A quarter of all males trapped in this group (4/16) were trapped both as juveniles and adults in Group H. As with similar animals in the anubis groups, we cannot tell which if any of these had immigrated as young juveniles, although their distinctive hybrid appearance suggested that they were natal. Many of these males are known from microsatellite analysis (BERGMAN, 1998) to have fathered offspring in Group H. One was first trapped at 4 years of age in 1991, then 4 and 7 years later, by which time he had fathered at least 3 infants. Four other males were trapped twice, initially as immatures, and subsequently as adults with their full dentition, but still under 10 years of age, and three of these had sired offspring in the group.

The low rates of migration among Group H animals as a group, when compared with anubis, are also apparent statistically. If the parameters TX ("taxon", 1 = anubis, 2 = hybrid) and MOVE ("whether the animal moved since last capture," 2 = "stayed", 3 = "moved") are treated as continuous variables, they can be included with AGE (estimated age in months) and INT (months since last capture) in a correlational analysis. Unsurprisingly, MOVE is highly correlated with both AGE and INT in a partial correlation controlling for group membership. However, when AGE, INT, and group membership are all controlled for, MOVE is significantly (negatively) correlated with TX ($r = -0.17$, $p = 0.029$, df = 162), indicating a lower rate of migration by hybrids. Since most of the retrapped hybrids in our sample were trapped in Group H, exactly the same result is obtained if those trapped in other groups are excluded.

Developmental correlates of contrasting dispersal regimes

As noted in our previous study (JOLLY and PHILLIPS-CONROY, 2003), adult male anubis are significantly heavier than hamadryas, due largely to an increase in mass between age classes 4 and 5 which is not seen in hamadryas. Hamadryas males in ageclass 4 have achieved almost 85 % of adult mass, compared to about 79 % in anubis (Table 1). Figure 2a shows that the slopes of the hamadryas and anubis curves track each other until about 72 months of age, when growth begins to slow in hamadryas males. This is illustrated in Figure 9a where average weight is plotted in

two year intervals. In the 73-96 month interval, or late subadult stage, hamadryas growth slows relative to anubis. Figure 2 also illustrates another difference between the taxa: after 10 years of age, hamadryas males show no further growth in body mass, but anubis males continue to show an increase.

Growth in grams/day was calculated by subtracting the average weight of animals in successive two year intervals and dividing by the number of days (Figure 9B.) Growth in male hamadryas peaks in interval 2 (approximately 48-72 months of age) at a little over 8gms/day, and then the rate of growth decreases until it virtually ceases by 120 months of age. Male anubis show their maximum growth later than hamadryas, as older subadults, between 73-96 months when their maximum growth is approximately 10gms/day. They continue to grow in the 12-14 year age interval, though much more slowly.

As we previously showed (JOLLY and PHILLIPS-CONROY, 2003), hamadryas and anubis differ significantly in adult testicular size. Mean testicle volume is 26.77 cc in hamadryas, and 44.69 cc in anubis (K-W p<0.001). Testis size does not differ significantly between the taxa until age class 5, but by age class 4, there is a clear difference in their relative completed growth: hamadryas males in this age class have almost achieved their final testicle size (97.1 %) whereas anubis males have achieved 72 %. This difference in timing is also detectable in the preceding age class, where hamadryas testes are 54 % of their final size, compared with anubis at 30%. Figures 3 and 9C illustrate that hamadryas testicular growth levels off in this late subadult period, while anubis continue to grow in testicle size for a number of years and show a second burst in testis growth when they are 12 -14 years of age. Figure 9D shows that hamadryas testis growth is at its maximum in intervals 1 and 2 and declines sharply in interval 3. The growth rate of anubis male testes exceeds hamadryas across all intervals, peaks in interval 2, and continues to decline until it approximates hamadryas growth in interval 4. The combination of these patterns of growth in body and testis size translates into significant difference between hamadryas and anubis in the testis size/body mass relationship (Tables 1, 3). Adult male anubis have a much higher testis size:body mass ratio (2.10 vs. 1.29), a statistically highly significant difference. However, as Figure 4 illustrates, until about 4-5 years of age juvenile hamadryas actually have testes that are larger for their body mass.

The growth trajectories for maximum girth in male anubis and hamadryas (Figure 5) are almost coincident over much of their length. The curves for arm and thigh circumference also closely track each other until about 100 months, but there is a suggestion that hamadryas males have completed more of their final growth earlier (i.e., in age class 4). The LOWESS curves beyond the normal cessation of skeletal growth at about 120 months suggest that hamadryas lose more body mass and limb muscularity as they become aged. Maximum girth does not show any clear taxon-specific pattern of change, but this is probably not surprising since this dimension largely reflects the bony elements of the axial skeleton.

Examination of the relative timing of canine to molar eruption showed that male anubis and hamadryas differ significantly in this feature (Figure 10). The trend is visible in age class 3, but the difference becomes more obvious, and is statistically significant, only in age class 4 when third molars are beginning to erupt, at around 8 years of age (An: HA Mann-Whitney p= 0.002) (Figure 10).
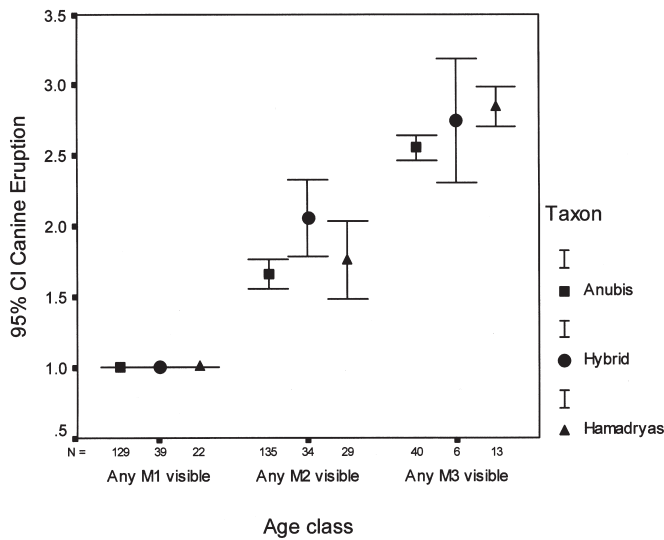
Fig. 10: Relative timing of canine eruption in anubis, hamadryas and hybrids.

Hybrids: The hybrids exhibit idiosyncratic patterns of growth and development that are neither exactly like either of the parental populations, nor intermediate between them, but combine some elements of each parental pattern with other features that are unlike either. Like anubis, hybrids have attained only 79 % of their full adult body mass by age class 4. They resemble hamadryas in that their growth trajectory slows in the late subadult stage, at 73-96 months,(when Mann-Whitney tests show hybrids are significantly different from both anubis and hamadryas males [<.0001 and .013 respectively]) , but then apparently returns to an anubis-like pattern with a dramatic growth spurt that brings them to full adult mass in the final two year interval. This final body mass is, however, significantly less than either anubis and hamadryas males (Tables 1, 3, Figure 8). The idiosyncrasy of the hybrids is expressed, also, when their gain in body mass is expressed in grams per day. At the age when anubis and hamadryas growth is at or near their peak, hybrid growth apparently slows, but then rebounds significantly in the following interval. As shown in Figure 2, hybrid males, like hamadryas but not anubis, decrease in body mass in their post-prime years.

In both mean adult testicle volume (44.15 cc.) and in the shape of the trajectory of testicular growth, hybrids resemble anubis rather than hamadryas (Figures 3 and 9C). That is, rather than leveling in age class 4, hybrid testicular volume undergoes a growth spurt late in development. Interestingly, however, the curve for hybrid males is displaced to the right of that for anubis; thus, in a pattern recalling the precocious growth of hamadryas testes, hybrid males achieve their peak growth in interval 3. With their anubis-sized testes and small body mass, adult hybrid males have a higher mean testis size:body mass ratio (2.38) than either of the parental populations (Table 1).

As might be expected from their low body mass, hybrid males also have relatively small limb and trunk girths. The curve depicting growth in maximum girth with age in hybrid males (Figure 5) lies below those for the parental forms. Residuals from the common regression line are significantly different from those of anubis in age classes

2 and 5 (Table 3). The plots of growth by two year intervals confirm that the pattern of hybrid growth deviates from anubis and hamadryas males, particularly in the 72-96 month interval, where the differences are statistically significant (AN-HY: p< 0.001; HY-HA: p= 0.007).

The LOWESS curves of arm and thigh circumferences similarly show smaller dimensions for age in the hybrids than in either of the parental forms. Hybrids of age class 5 have smaller limb circumferences than either anubis or hamadryas (significantly so for thigh (K-W = 0.023), but, unlike hamadryas, do not show the tendency to complete growth in age class 4. The plots of growth in two year intervals for arm and thigh circumferences again point to a changing pattern of growth in hybrid males in the crucial 72-96 month period. Mann-Whitney U tests show that arm circumference is less in hybrids than in anubis (p< 0.001) or hamadryas (p= 0.005). Thigh circumference of hybrid males is significantly less than in anubis (p< 0.001), but does not differ significantly from hamadryas. Like hamadryas males, hybrid males lose limb girth in old age.

As shown in Figure 10, hybrid males resemble hamadryas in erupting their canine teeth relatively earlier than anubis males, although the difference is significant only in age class3 (p= 0.006).

Discussion

The direct evidence of observation, together with inferences from retraps and mitochondrial haplotype distributions (NEWMAN, 1997; JOLLY et al., 2003, in prep. strongly suggest that in Awash anubis baboons, male dispersal follows the pattern described from populations elsewhere in East Africa (SMUTS, 1985; STRUM, 1987; SAPOLSKY, 2001; PACKER ,1979). Male anubis baboons disperse natally as young adults or, quite often, as juveniles, and secondary movements between troops are frequent, even into old age. The genetic evidence suggests that, as observed in other populations, males probably disperse non-randomly, tending to enter a group where they already have a male (matrilineal) relative. Inter-troop movement may be facilitated in Awash compared to some other populations, since the roosting sites of troops, spaced linearly along the riverine forest belt, are rarely changed, and are separated by only a few hundred meters. This distribution affords many opportunities for males to assess the attractiveness of neighboring troops, and also to move directly from one troop to another, without an intervening, dangerous, period of extra-troop life. Some males, however, clearly disperse over much longer distances, as shown by the anubis that attached themselves to hamadryas groups at Filwoha. Even in this marginal habitat for the taxon, therefore, anubis baboons show no discernible tendency to converge on the philopatric behavior of hamadryas.

Theory suggests that dispersal is favored, both as an individual response, and a population-level evolutionary adaptation, when the "quality" of habitat patches varies over time, as long as an individual organism can assess the quality of neighboring habitat patches, and can move adaptively between them (HANSKI, 2001). The quality of a habitat patch is defined by the fitness it confers on its occupants, determined by the concentration of resources in the patch and the intensity of competition for the resources. For male mammals of facultatively polygynous species, including baboons, potential mates are generally considered the critical resource. For savanna

baboons, the attractiveness of a troop to a potential immigrant should be a function of the number of (unrelated) females and potential rival males it contains, with the relatedness of the other males to the immigrant mitigating their negative impact on his fitness. These demographic qualities of a troop are ephemeral, so that a strong propensity to disperse, combined with an ability to monitor the critical parameters in neighboring troops is clearly advantageous. Our results on the relatedness of immigrant male anubis, and more extensive data from yellow baboons (ALBERTS and ALTMANN, 1995, 2001), provide empirical evidence that dispersal in savanna baboons corresponds to the predicted pattern.

The observations made since 1990 confirm our earlier findings (PHILLIPS-CONROY and JOLLY, 1991, 1992) that some adult males must disperse from hamadryas groups living close to the contact zone, since they appear as immigrants in anubis troops. The exact rate of cross-taxon dispersal cannot be calculated, since we do not know the total membership of the potential source populations, but it is unlikely to be high, since the anubis range is flanked to the north by extensive hamadryas populations. Rather than simply being transient mate-raiders (KUMMER, 1988, 1995), some of the immigrants take up residence in anubis groups and spend the rest of their lives there – in the longest documented cases, at least 10-12 years. Since these immigrant adult males were of widely disparate ages, including some that were in or past middle age, we (PHILLIPS-CONROY and JOLLY, 1991, 1992) previously surmised that they migrated because they had failed to establish, or had lost, an OMU in their natal band. The latest observations show that juvenile males – some as young as 2½ years – also transfer from hamadryas to anubis groups. Some leave again as juveniles, while others stay long enough to grow to adulthood, and may even transfer a second time to another anubis troop. Although studies of other hamadryas populations, distant from the contact zone (SIGG et al., 1982; ABEGGLEN, 1984) may have overlooked some male emigration by attributing disappearances to deaths, we have no reason to doubt their general conclusion that almost all hamadryas males are philopatric. Why, then, do some Awash hamadryas show an anubis-like pattern, dispersing, joining a new group and sometimes even changing group more than once? We can imagine several possible explanations. One is that some Awash hamadryas have acquired "dispersal genes" by hybridization with anubis. This seems unlikely, if only because most of the actual migrants show fewer phenotypic signs of admixture than most members of Groups A and K, which are geographically closer, and which might, on this hypothesis, be expected to supply most of the migrants. A second explanation is ecological; that dispersal is ecologically advantageous in the Awash setting, and therefore has become more common among hamadryas, either by natural selection, if innate, or by individual decision, if plastic. It is, however, hard to discern what the ecological element might be, since the habitat of hamadryas in Awash is well within the range of habitats occupied by hamadryas elsewhere.

Our preferred explanation is that an anubis group exerts a powerful attraction on hamadryas males, by virtue of its "unattached" females. In a hamadryas band, all females are normally attached to an adult male in a jealously-guarded OMU. Unattached adult females, potential mates for bachelor males, are present only rarely, at the dissolution of an OMU, and in a matter of minutes they have been "recruited" by a new leader. Unlike male savanna baboons, male hamadryas are intensely attrac-

ted to adult females whether or not the latter are periovulatory. A male hamadryas encountering an anubis troop would therefore be presented with a supernormal stimulus in the form of many, apparently available, females, and we suggest that this may overcome the male's inherent tendency to philopatry. In hamadryas bands, quite young juvenile males often attach themselves to an adult male as a "follower" of the OMU. It is perhaps significant that all the cases of juvenile hamadryas immigration involved anubis troops where at least one adult hamadryas was already in residence, although in all cases the juvenile transferred alone, not in company with an adult.

Although the migration of some male hamadryas in the border zone indicates that there is plasticity in its expression, hamadryas philopatry remains a fundamental and distinctive apomorphy of the taxon and is associated with physical and developmental characteristics that almost certainly have a genetic basis. We have previously commented on the apparent precocity of testicular development in hamadryas compared to anubis, and suggested that this correlates with the earlier initiation of reproductive behavior, made possible by growing up among relatives rather than competitors. Data presented here suggest that while measures of muscularity are not similarly advanced, the eruption of the canine teeth, which are highly sexually dimorphic, and may also be coupled to hormonal maturation, may also be somewhat accelerated in hamadryas. In addition, there is evidence that the philopatry of hamadryas baboons, like a tendency to late natal dispersal in individual male rhesus macaques (*Macaca mulatta*) (MEHLMAN et al., 1995) may be associated with higher serotonin metabolite levels in the cerebrospinal fluid of hamadryas compared to anubis males (KAPLAN et al., 1999 a,b). It therefore appears that hamadryas and anubis, respectively, exhibit complexes of contrasting character states that are adaptively related, respectively, to a norm of philopatry, and to a tendency to disperse that may be even more pronounced than in other savanna baboons (ALBERTS and ALTMANN, 1995, 2001). These internally consistent and co-adapted complexes are apparently disrupted in hybrids. In the particular gene pool represented by the Group H animals, the hybrid genotype yields a combination of the late testicular growth spurt characteristic of anubis which, we argue, is correlated with a reproductive career initiated after dispersal, with the testicular precocity associated in hamadryas with juvenile sexuality (JOLLY and PHILLIPS-CONROY, 2003). There is no reason to suppose that this maturational track (if indeed it is representative of a true longitudinal growth and not a cohort-driven artifact of our cross-sectional dataset) is adaptive to the dispersal regime prevalent in Group H, which seems to be predominantly philopatric. It remains to be demonstrated whether the disruption of dispersal-related adaptive complexes plays a role in the spatial limitation of the Awash hybrid zone.

permission granted by successive General Managers of the Ethiopian Wildlife Conservation Organization; the collaboration of Addis Ababa University; and, the invaluable practical assistance of the Wardens and Staff of the Awash National Park.

References

ABEGGLEN, J.-J.: On Socialization in Hamadryas Baboons: A Field Study. London: Associated University Presses (1984).

ALBERTS, S.C. and ALTMANN, J.: Balancing costs and opportunities: dispersal in male baboons. Am. Nat. (1995) 145: 279-306.

ALBERTS, S.C. and ALTMANN, J.: Immigration and hybridization patterns of yellow and anubis baboons in and around Amboseli, Kenya. Am. J. Primatol. (2001) 53: 139-154.

ALDRICH-BLAKE, F.P.G., BUNN, T.K., DUNBAR, R.I.M. and HEADLEY, P.M.: Observations on baboons, *Papio anubis*, in an arid region in Ethiopia. Folia Primatol. (1971)15: 1-35.

BEEHNER, J. (in prep.): Social behavior among females of mixed ancestry in a baboon hybrid zone, Awash National Park, Ethiopia (2003).

BERGMAN, T.: Mating behavior and reproductive success of hybrid male baboons. Unpublished PhD dissertation. St. Louis: Washington University (2000).

BEYENE, S.: The role of female mating behavior in hybridization between anubis and hamadryas baboons in Awash, Ethiopia. Unpublished PhD dissertation. St. Louis: Washington University (1998).

BRETT, F.L., JOLLY, C.J., SOCHA, W. and WIENER, A.S.: Human-like ABO blood groups in wild Ethiopian baboons. Yearbook of Physical Anthropology *(*1977) 20: 276-289.

BRETT, F.L., TURNER, T.R., JOLLY, C.J. and CAUBLE, R.G.: Trapping baboons and vervet monkeys from wild, free-ranging populations. Journal of Wildlife Management (1982) 46: 164-174.

HANSKI, I.: Population dynamic consequences of dispersal in local populations and metapopulations. In: CLOBERT, J., DANCHIN, E., DHONDT, A.A. and NICHOLS, J.D. (eds.): Dispersal. Oxford: Oxford University Press (2001): 283-298.

HAPKE, A., ZINNER, D. and ZISCHLER, H.: Mitochondrial DNA variation in Eritrean hamadryas baboons (*Papio hamadryas hamadryas*): life history influences population genetic structure. Behav. Ecol. Sociobiol. (2001) 50: 483-492.

JOLLY, C.: A suggested case of evolution by sexual selection in primates. Man (1963): 177-178.

JOLLY, C.J.: Species, subspecies, and baboon systematics In: KIMBEL, W.H. and MARTIN, L.B. (eds.): Species, Species Concepts, and Primate Evolution New York: Plenum Press (1993): 67-107.

JOLLY, C. and BRETT, F.L.: Genetic markers and baboon biology. Journal of Medical Primatology (1973) 2: 85-99.

JOLLY, C. and PHILLIPS-CONROY, J.E.: Testicular size, mating system and maturation schedules in wild anubis and hamadryas baboons. Int. J. Primatol. (2003) 24: 124-142.

JOLLY, C.J., NEWMAN, T.K., BRETT, F.L., PHILLIPS-CONROY, J.E. and DISOTELL, T.R. (in prep.): Mitochondrial variation and intertroop movements in baboons. (2003).

KAPLAN, J., PHILLIPS-CONROY, J.E., JOLLY, C.J., FONTENOT, M.B. and MANN, J.J.: Cerebrospinal fluid monoaminergic metabolites differ in wild anubis, hamadryas and hybrid baboons, possibly reflecting variation in life history. Am. J. Phys. Anthropol. (1999a) 108: 164.

KAPLAN, J.R., PHILLIPS-CONROY, J.E., FONTENOT, M.B., JOLLY, C.J., FAIRBANKS, L.A. and MANN, J.J.: Cerebrospinal fluid monoaminergic metabolites differ in wild anubis and hybrid baboons: possible relationships to life history and behavior. Neuropsychopharmacology (1999b) 20: 518-524.

KUMMER, H.: Two variations in the social organization of baboons. In: JAY, P. (ed): Primates. New York: Holt, Rinehart and Winston (1968a): 293-312.

KUMMER, H.: Social Organization of Hamadryas Baboons. Chicago: Aldine (1968b).

KUMMER, H.: The social system of hamadryas baboons and its presumable evolution. In: BYRNE, R.W. (ed.): Baboons XII Congress of the International Primatological Society (1988): 43-73.

KUMMER, H.: In Quest of the Sacred Baboon. Princeton: Princeton University Press (1995).

MEHLMAN, P.H., HIGLEY, J.D., FAUCHER,I., LILLY, A., TAUB, D.M., VICKERS, J., SUOMI, S.J. and LINNOILA, M.: Correlation of CSF 5-HIAA concentration with sociality and the timing of emigration in free-ranging primates. Am. J. Psych. (1995)152: 907-913.

NAGEL, U.: A comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. Folia Primatol.(1973) 19: 104-165.

NEWMAN, T.K.: Mitochondrial DNA analysis of intraspecific hybridization in *Papio hamadryas anubis* and *Papio hamadryas hamadryas* and their hybrids in the Awash National Park, Ethiopia. Unpublished PhD dissertation. New York: New York University (1997).

PACKER, C.: Inter-troop transfer and inbreeding avoidance in *Papio anubis*. Anim. Behav. (1979) 27: 1-34.

PHILLIPS-CONROY, J.E.: Dental variability in Ethiopian baboons: an examination of the Anubis-Hamadryas hybrid zone in the Awash National Park, Ethiopia. Unpublished PhD dissertation. New York: New York University (1978).

PHILLIPS-CONROY, J.E. and JOLLY, C.J.: Sexual dimorphism in two subspecies of Ethiopian baboons (*Papio hamadryas*) and their hybrids. Am. J. Phys. Anthropol. (1981) 56: 115-129.

PHILLIPS-CONROY, J.E. and JOLLY, C.J.: Changes in the structure of the baboon hybrid zone in the Awash National Park, Ethiopia. Am. J. Phys. Anthropol. (1986) 71: 337-350.

PHILLIPS-CONROY, J.E. and JOLLY, C.J.: Dental eruption schedules of wild and captive baboons. Am. J. Primatol. (1988) 15: 17-29.

PHILLIPS-CONROY, J.E., JOLLY, C.J. and NYSTROM, P.D.: Palmar dermatoglyphics as a means of identifying individuals in a baboon population. Int. J. Primatol. (1986) 7: 435-447.

PHILLIPS-CONROY, J.E., JOLLY, C.J. and BRETT, F.L.: Characteristics of hamadryas-like male baboons living in anubis baboon troops in the Awash hybrid zone, Ethiopia. Am. J. Phys. Anthropol. (1991) 86: 353-368.

PHILLIPS-CONROY, J.E., JOLLY, C.J., NYSTROM, P.D. and HEMMALIN, H.A.: Migration of male hamadryas baboons into anubis groups in the Awash National Park, Ethiopia. Int. J. Primatol. (1992) 13: 455-476.

PHILLIPS-CONROY, J.E., BERGMAN, T. and JOLLY, C.J.: Quantitative assessment of occlusal wear and age estimation in Ethiopian and Tanzanian baboons. In: WHITEHEAD, P.F. and JOLLY, C.J. (eds.): Old World Monkeys. Cambridge: Cambridge University Press (2000): 321-340.

PUSEY, A.: Sex-biased dispersal and inbreeding avoidance in birds and mammals. TREE (1988) 2: 295-299.

PUSEY, A.E. and PACKER,C.: Dispersal and philopatry. In: SMUTS, B.B., CHENEY, D.L., SEYFARTH, R.M., WRANGHAM, R.W. and STRUHSAKER, T.T. (eds.): Primate Societies. Chicago: University of Chicago Press (1986): 259-266.

REED, O.M.: *Papio cynocephalus* age determination. Am. J. Phys. Anthropol. (1973) 38: 309-314.

SAPOLSKY, R.M.: Stress, social status, and reproductive physiology in free-living baboons. In: CREWS, D. (ed.): Psychobiology of Reproduction: An Evolutionary Perspective. New York: Prentice Hall (1986): 291-321.

SAPOLSKY, R.M.: A Primate's Memoir. New York: Scribner (2001).

SHOTAKE, T.: Population genetical study of natural hybridization between *Papio anubis* and *P. hamadryas*. Primates *(*1981) 22: 285-308.

SHOTAKE, T., NOZAWA, K. and TANABE, Y.: Blood protein variations in baboons I. gene exchange and genetic distance between *Papio anubis*, *Papio hamadryas* and their hybrid. Japanese Journal of Genetics (1977) 52: 223-237.

SIGG, H., STOLBA, A., ABEGGLEN, J.-J. and DASSER, V.: Life history of hamadryas baboons: physical development, infant mortality, reproductive parameters and family relationships. Primates *(*1982) 3: 473-487.

SMUTS, B.B.: Sex and Friendship in Baboons. New York: Aldine (1985).

STRUM, S.: Almost Human: A Journey into the World of Baboons. New York: Random House (1987).

SUGAWARA, K.: Sociological comparison between two wild groups of anubis-hamadryas hybrid baboons. African Studies Monographs (1982) 2: 73-131.

SUGAWARA, K.: Ethological study of the social behavior of hybrid baboons between *Papio anubis* and *P. hamadryas* in free-ranging groups. Primates (1988) 29: 429-448.

SWEDELL, L.: Social behavior and reproductive strategies of female hamadryas baboons, *Papio hamadryas hamadryas*, in Ethiopia. Unpublished PhD dissertation. New York: Columbia University (2000).

WOOLLEY-BARKER, T.: Social organization and genetic structure in a baboon hybrid zone. Unpublished PhD dissertation. New York: New York University (1999).

ZAHAVI, A.: Mate selection - a selection for a handicap. Journal of Theoretical Biology (1975) 53: 205-213.

Correspondence to:
Dr. Jane E. Phillips-Conroy, Department of Anatomy and Neurobiology, Washington University School of Medicine, St. Louis, MO 63110, U.S.A.
E-mail: baboon@pcg.wustl.edu

DISPERSAL AND ENVIRONMENTAL DISTURBANCE IN JAPANESE MACA-
QUES (*MACACA FUSCATA*). FUKUDA, F.

Abstract

Presently, in every region of the nation, citizens can obtain news about wild Japa-
nese macaques (*Macaca fuscata*) invading not only the countryside but also urban
areas. As documented in the present report, these individuals are confirmed to be fe-
males as well as males. Female Japanese macaques are thought to be philopatric,
never leaving their natal troops, while males disperse from their groups of origin. In
order to clarify the topic of female dispersal in Japanese macaques, data for the
Hakone T troop of *M. fuscata* are presented. Three stages of troop size were discrimi-
nated: an increasing stage, a fluctuating stage, and a decreasing stage. In the latter
two stages, 17 adult females deserted the troop. Characteristics of these stages are
compared and presented with observations on male movements. Based upon the
present findings, it is hypothesized that female dispersal is caused by the shortage of
natural food resources resulting from habitat destruction.

Introduction

Appearance of Wild Animals Within City Limits

In the summer of 2002, one bearded seal appeared in the Tama River running the
boundary between Tokyo and Kanagawa prefectures. Becoming very popular, the
seal was followed every day by numerous TV cameramen, photographers, and
crowds of citizens, including all age classes. Affectionately, the seal was named
Tama-poo.

Nowadays, we Japanese can often get news about wild animals from the land and
sea (e.g., sika deer, wild pigs, black bears, and monkeys), although in recent years
news reports about macaques have become less frequent because citizens have ha-
bituated to the appearance of macaques within the city limits.

Japanese macaques (*Macaca fuscata*) invade not only the countryside (e.g., culti-
vated areas, farms, and orchards) but also urban areas in every region of the nation.
Macaques are highly conspicuous. Solitary macaques, but not troops, appear and
wander through metropolitan areas such as Tokyo and Yokohama. For example, a
very famous young adult female named Azami moved about 20 km from Hachiouji
city to the center of Tokyo for three months between June and August 1999. Accord-
ingly, many TV reporters and photographers followed her and broadcasted her every
move. Moreover, in 2000, more than fifteen macaques appeared in the heavily popu-
lated coastal area of Kanagawa prefecture. Among these macaques, some sightings
were lone male or female individuals or small-sized groups of 2-3 animals, including
female, all-male groups, and/or a few mother-infant dyads. Until 30 years ago, how-
ever, most Japanese macaques appearing in urban areas were males, raising the
question: What accounts for this changed pattern?

For the country as a whole, arch-shaped mountains run along the narrow Japanese landscape, and ≈80 % of the country is mountainous and forested. Where inhabitable and arable, people are found, living in close proximity to habitats of Japanese macaques. Because of this circumstance, macaques have sometimes appeared in the rural countryside of Japan since ancient times (MITO and WATANABE, 1999). However, most reports from rural areas also indicated that these animals were primarily males. The appearance of female macaques in urban and rural areas is, then, relatively recent. *M. fuscata* females are generally considered philopatric, never leaving their natal troops (KAWAI, 1969; ITANI, 1987; also see PUSEY and PACKER, 1987). What factors would cause a young adult female like Azami to desert her troop, moreover, to move alone? Why did a lone female macaque appear in the center of a city? Why did many macaques, including females, appear on the coast of Kanagawa prefecture? These and related questions motivated the research presented in this paper.

Japanese Macaque Social Organization

For our studies, monkeys were marked and aged according to the methods described by FUKUDA (1982, 1988). Our work generally confirmed previous reports on *M. fuscata* (e.g., SUGIYAMA, 1960; see MELNICK and PEARL, 1987). Japanese monkeys, well-studied in the field, are organized into multimale-multifemale troops comprised of several female matrilines and a few male immigrants. Female offspring live in their natal troop throughout their lives, but male offspring emigrate from their natal troop before sexual maturation. Emigrating males become solitary and/or form temporary all male groups with other males, including unrelated males. After 6 months or so, males immigrate into troops adjacent to their natal troop, and young males emigrate from their natal groups when they are 5 or 6 years old, remaining in a new troop for 3 years or more (FUKUDA, 1982). New troops are formed by a process of troop fission, occurring when troop size exceeds some threshold limit (SUGIYAMA, 1960; FURUYA, 1968). Moreover, troop fission creates kin groups of higher and lower rank (KOYAMA, 1970; OI, 1988), and troop members move and forage together on a home range. Members of the well-studied T troop in Hakone area have been known to fission-fusion habitually (FUKUDA et al., 1974; FUKUDA, 1988). During the mating season, between the end of September and the end of March in all localities (KAWAI et al., 1967), solitary males sometimes approach troops (KAWAI, 1969). The mating system is promiscuous (ENOMOTO, 1978; TAKAHATA, 1982), whereby both sexes copulate with multiple partners during a mating season. The age of primiparous females ranges from 4-8 years, depending upon nutritional state (MORI, 1979).

Female Dispersal Clarified in the Hakone T Troop of Japanese Macaques

The following discussion is based upon observations of male and female dispersal from the Hakone T troop of Japanese macaques (males: FUKUDA, 1982; females: FUKUDA, 1983 [both in Japanese with English summary]). My colleagues and I systematically observed several troops of Japanese macaques in the Hakone Mountains for at least 14 years between 1966 and 1980 and have continued to observe them intermittently since 1981. Hakone Mountains, located in the western part of Kanagawa prefecture, is approximately one and one-half hours by car from the Tokyo

metropolitan area (Fig. 1). Two troops (T and P) inhabited the region when I began observations. T and P troops had been provisioned between 1956 and 1976, and between 1964 and 1974, respectively. The size of T troop was about 35 in 1956 when provisioning started. After that time, troop size increased and nearly doubled during the first 11 years to 69 individuals in 1966 when my observations began. In 1967, H troop was formed by two adult males originating from P troop, three adult females from T troop, and seven unknown animals. Moreover, the size of T troop continued to increase until 1969 (95 macaques). Between 1969 and 1974, troop size fluctuated around 100. Then, from 1974 to 1978, troop size fell drastically to 57 animals.
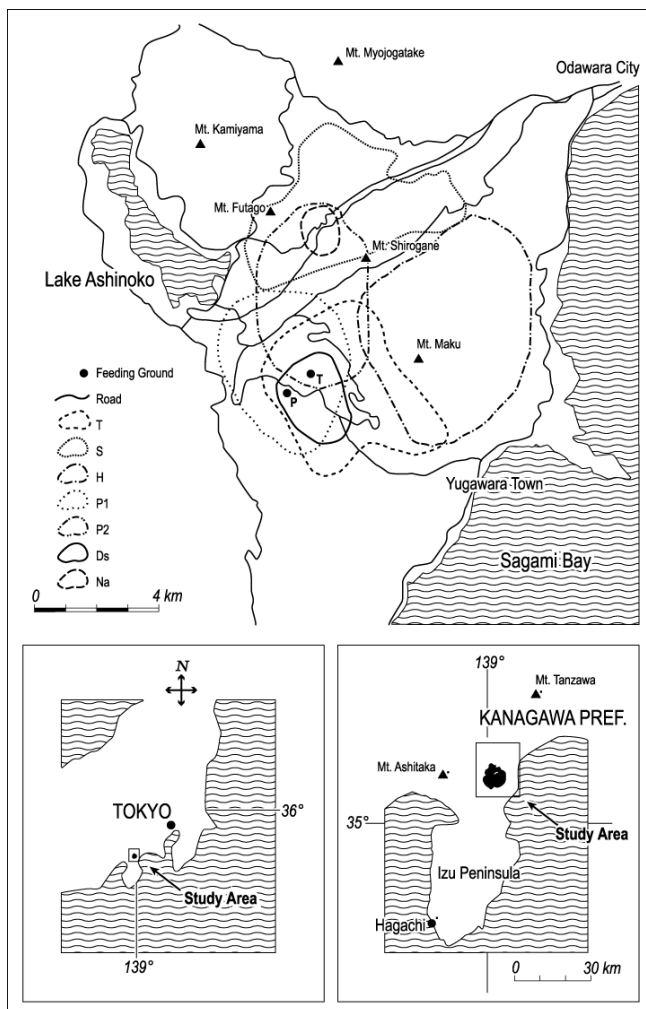

Fig. 1: Ranges of seven troops in the Hakone Mountains (January 1975-December 1977). Locations of Tokyo and the study area are indicated the lower figures.

Thus, these 13 years from 1966 to 1978 can be classified into three periods: an increasing period before 1968, a fluctuating period from 1969 to 1974, and a decreasing period from 1975 (Fig. 2). Naturally, the increasing factors of troop-size are

based on high birth rate, younger primiparous age, low infant mortality, etc. These parameters were caused by good nourishment as a result of provisioning. On the other hand, P troop fissioned into two troops (P1 and P2) in November 1974, after the cessation of artificial feeding in September 1974. Moreover, S troop had been found in the Hakone area in 1969. Many tourists visit the Hakone area, where a recreational area is located that has been designated a national park since 1936. As a result, macaques in all five troops (T, P1, P2, H, and S) have been conserved but were occasionally given food from tourists along roadways (see cover photo).
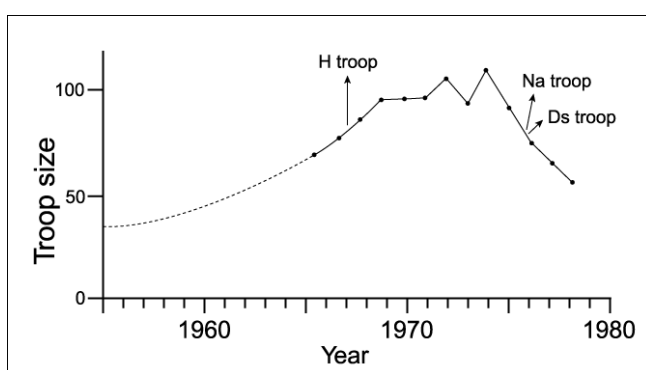

Fig. 2: Changes in T troop size and new troop fissioning from this troop.

Features of Females Who "Disappeared" and "Deserted"

During the eight years from April 1971 to March 1979, thirty-five females at least five years of age disappeared from T troop (see SUGIYAMA, 1982). These females occupied almost all age classes. However, it should be noticed that, among the four disappearances of females more than 20 years of age, all were found alive. Here, "disappearances" means females disappearing from T troop and never returning to it again (including females which deserted, were killed, captured, or were dead or alive but not found). "Deserters" means animals that were found alive after disappearance. There was no significant difference for number of disappearances and/or deserters among three age classes (5-9 years of age, 10-14 years of age, and >15 years of age [Table 1]). Deserters originated from thirteen kin groups (48.1 %) of all twenty-seven kin groups in the T troop. Among all deserters, ten (55.6 %) were matriarchs of each kin-group, six (33.3 %) were the eldest daughters of their matriarchs, and the remaining two were a granddaughter of her matriarch and the second daughter of her matriarch, respectively (cf. FUKUDA, 1983).

Of all deserters, two were senior females who had not given birth, one for six and one for three years before their desertion. The remaining fifteen (except one female 5 years of age) gave birth within two years before their desertions. Three females deserted from the troop with an infant (< l year old). Fifteen females deserted alone from the troop. However, some relatives of four of the female deserters disappeared almost simultaneously from the troop. There was a strong tendency for most deserters (82.4 %) to issue from lower rank kin groups in T troop (χ^2= 6.370, p<0.02, df= 1; see FUKUDA, 1983).

Table 1: Comparison of adult female residents and disappeared individuals and/or deserters by three age classes in T-troop for seven years.

Age in years	Adult Female-Years	Number of Disappeared Individuals	Expected Value	Number of Deserters	Expected Value
5-9	118	6	7.7	7	8.2
10-14	59	4	3.9	4	4.1
15 & over	83	7	5.4	7	5.7
Total	260	17	17.0	18	18.0

As reported by FUKUDA (1983), the mean size of kin groups of the troop in April 1972 was 3.5 (N=27 kin groups). The mean size of kin groups which females deserted was 3.8 (N=13 kin groups), occupying about half of the members of T troop. Since March 1979, five of these 13 kin groups have become extinct from the troop, and the remaining eight kin groups occupied 35 % of the members of the troop. The mean size of these eight kin-groups decreased to 2.6 animals (N=8 kin groups). The ratio of disappearances/deserters was closely related to the food supply, and there was a significant inverse correlation between artificial food supply and number of adult females who disappeared and/or deserted from the troop(N= 5, r_s= 0.90, p<0.05, Table 2). Thus, the lower the food supply in a year, the more females disappeared and/or deserted compared with the number of those disappearing and/or deserting in the previous year (cf. FUKUDA, 1983).

Table 2: Relationships between artificial food supply and number of adult females disappeared and/or deserted from T-troop.

	1972	1973	1974	1975	1976	1977
Difference*		31	-116	-55	26	-9
Number of Females	3	0	10	8	3	9
*Difference: (per capita food supply of the surveyed year) - (per capita food supply of the previous year). Per capita food supply: refer to Table 4.						

Conditions after Desertion

All 18 female deserters were found in Hakone area, which we had been studying. Eighteen adult females were located immediately after desertion and were classified into eight categories from the viewpoint of size, age-sex composition and group history. In other words, the categories were: remaining alone (n = 2) or only with her infant (n = 1), forming a pair with an adult male (n = 1), forming new troops with members of her previous troop or with strangers (n = 2), immigration into an adjacent troop (n = 4), disappeared with collapse of subgroup of T troop during mating season (n = 6), and repeated absence from T troop for more than one month (n = 2).

Eight deserters formed the new troop, and 4 immigrated into an adjacent troop (i.e., one who was first found alone and three who formed the new troop). Out of 15 adult female deserters, 5 gave birth to offspring. Their babies had been conceived in other troops (Na, Ds and P-2). Among five deserters found out of the range of T troop,

1 was alone, 2 formed a new troop, and 2 immigrated into another troop. Among 13 deserters found in the range of T troop, 5 entered two subgroups of T troop and were lost after disruption of these subgroups. Two deserters who repeatedly deserted from and returned to T troop were lost after their final desertion. There is a high possibility that these seven female macaques not only went outside the range of T troop but also outside the Hakone area. They could easily have been found if they had remained in the Hakone area because they were accustomed to obtain food from tourists along the roadside.

The formation of a new troop of Japanese macaques is based on a troop fissioning into two troops when the troop-size exceeds some threshold size (SUGIYAMA, 1960; FURUYA, 1968; KOYAMA, 1970). However, new troop formation has not been reported, only the process of troop fissioning (FUKUDA, 1983, 1988, 1990). Accordingly, the following describes new troop formation (Ds & Na) and the immigration into other troops by female deserters.

Ds troop: Six adult females, who left independently from T troop over a period of three years and two months between February1975 and April1978, formed a new troop (Ds) with an adult male. Ds troop was formed February 1976 and continued for more than five years and three months. For this period, there were three aggregation (troop formation) phases and two dispersion phases. Every aggregation phase started in the latter half of the mating season, and dispersion phases occurred during birth seasons. During the aggregation phases, a pair was formed comprising an adult male from a troop other than T troop and an adult female who had deserted from T troop. This pair was joined by a second female who had deserted from T troop. The female-female association took place without agonistic behaviors. These females, however, were observed to attack and/or chase an adult male out of the newly formed group. However, a strong bond existed between the original male and female pair, and no blood relationship existed among females who formed the Ds troop. The home range of this troop was very small, about 4 km^2, which formed part of the range of T troop.

Why wasn't Ds troop's home range larger? Ds troop members frequently appeared nervous about their surroundings, possibly because of their proximity to T troop. As soon as the members of Ds troop noticed members of other troops, they ran away. Probably, if a new troop like Ds were to form in areas uninhabited by no other Japanese macaques troops, the new troop would forage over a large range and troop size would increase.

Na troop: Na troop was comprised of four adult males and four adult females—two females of unknown origin and two female deserters from T troop. Na troop was formed in January 1976 and fused into P2 troop in January 1978. The fusion between members of separate troops occurred without apparent tension, and females of different origin groomed each other frequently. While Na troop was forming, there existed a strong affiliative relationship between the two female deserters from T troop and a male. These relationships remained stable, even after the fusion of the females from separate troops. The range of Na troop never overlapped that of T troop. It was about 4 km^2, located in the center of the range of S troop. The fusion of two troops of Japanese macaques has not previously been reported.

Emigration to other troops: Two females who had deserted from T troop transferred into P2 (excluding two females from Na troop). One of these females remained in P2 troop for about 3 months and the other for about 17 days. The 7 year old son of one of these female transfers had already emigrated into the troop. However, there was no affiliative behavior between mother and son such as grooming, and the son transferred into P1 troop two weeks after his mother emigrated into the troop. The son's transfer from P2 troop into P1 troop is an interesting case of secondary dispersal. This son avoided his mother, not displaying agonistic behavior towards her or other P2 troop members. Another female participated in the formation of Ds troop and transferred into P2 troop during the first dispersion phase of Ds troop. There was no affinitive behavior between this female and the former, emigrant female.

Troop Desertion and Troop-Shifting by Females Other Than T Troop Females

Aside from the origin of T troop, it was confirmed that 8 adult females deserted from one troop to another troop (Table 3). Fig. 3 shows the troop shifting of these individuals. Two adult females, (Hageko—her original troop unknown—and Punkt—who originated from P2 troop), stayed in T troop for 2 months and one and half months, respectively. Two other adult females, (Nanako and A—their original troops unknown), participated in the formation of Na troop. One adult female, (Nimiko—her original troop unknown), moved in and out of more than one troop (P1, P2, and Na), and Shaku, more than 20 years of age, was absent from her P2 troop for one and half years. During this time, she was discovered with Nimiko for only one
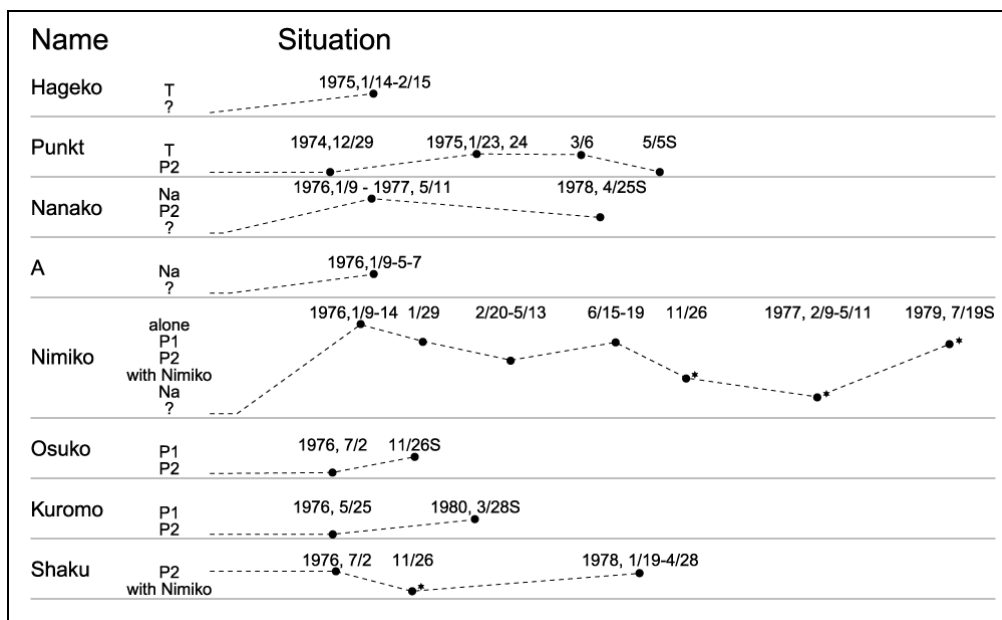

Fig. 3: Troop shifting by adult females. T, P2, Na, and P1 indicates individual females symbolized by their troop of origin. Nimiko and Shaku were found together on November 26, 1976. Alone= found alone. ?= troop of origin unknown.

day; however, in general her whereabouts could not be determined. Although the original troops of Hageko, Nanako, A, and Nimiko were unknown, there is a possibility that they came from the neighboring area (i.e., the Izu Peninsula, the Tanzawa Mountains, and Ashitaka Mountain [see Fig. 1]), because almost all macaques, except infants less than one year of age, in the Hakone area could be recognized individually. With the exception of an old female (Shaku), the age of seven other females were estimated to be between 8 and 13 years of age compared with females of T troop. Nimiko and Shaku moved with their babies, and others moved alone. The troop shifting by these females seemed to take place without tension, because female immigrants were never attacked by other troop-members.

Compaisons Between Dispersers in a Fluctuating and a Decreasing Period

The artificial food supply per capita per diem between 1972 and 1977 is shown in Table 4. The average food supply in 1972 and 1973 was about 200 Cal, that in 1974 decreased to 112 Cal, while after 1975 it decreased to less than half the original amount (to about 70 Cal). The annual amount of food supply before 1971 appeared to be the same as that in 1972 (personal communication from an officer of the Yugawara town office, FUKUDA, 1988). The drastic decrease of troop-size began in 1974, when the food supply was decreased to almost half that of the previous year. On the other hand, as already described, P troop fissioned into two troops (P-1 and P-2) after 1974 at which time the artificial food supply stopped.

It is suspected that the increase and decrease of troop size and the troop fission were affected by the amount of food supply. Female desertions from T troop were observed from 1969 to 1979, that is, after a fluctuating period and a decreasing period. Thereafter, the number of disappearances of females five years of age and older in the fluctuating period was compared with that in the decreasing period (Table 3). The percentages (57 %) of deserters found with respect to all disappearances in 1971-1974 was higher than those (45 %) in 1975-1977. Similarly, for disappearances of natal males two years of age and older, the percentages (38 %) of deserters found with respect to all disappearances in 1971-1974 were also higher than those (21 %) in 1975-1977. There was no significant difference between both periods for either sex. However, these findings suggest that the scarce food supply may have induced animals to disperse to distant areas other than into adjacent troops in the Hakone area, although there is no concrete evidence for this possibility (see below).

Among resident animals in T troop, the number of non-natal males exceeded that of natal males throughout the seven years (Table 4). "Resident" means 5 years of age and older natal and non-natal males seen in T troop from the previous year. The comparison of non-natal males to all resident males during 1971-1974 was significantly lower than that during 1975-1977 (Mann-Whitney U - test, $U = 0$, $p < 0.05$). On the other hand, among all non-natal males, the comparison of newcomers during 1971-1974 was significantly higher than that during 1975-1977 ($U = 0$, $p < 0.05$). The shortage of artificial food supply during 1975-1977 could have caused the number of newcomers to decrease and the ratio of non-natal males to all resident males to increase. This suggests that the food shortage might have encouraged natal males to desert the study troop while non-natal resident males remained in the troop. One factor, possibly encouraging dispersal from the natal troop by males, could have been the abundance and quality of food. However, the dispersal of non-natal males is probably also based on factors other than food.

Table 3: Number of deserters[1] in all disappearances in 1971-1974 and 1975-1977.

	Deserters		Disappearances		Rate[2] of Deserters	
	Males	**Females**	**Males**	**Females**	**Males**	**Females**
1971-1974	10	8	26	14	0.38	0.57
1975-1977	3	9	14	20	0.21	0.45
Total	13	17	40	34	0.325	0.50

[1]Animals which were found alive in the Hakone area.
[2]Rate of deserters in terms of the disappearances: Males: two and more than two years old; Females: five and more than five years old.

Table 4: Residents, newcomers, disappearances, and amount of artifical food supply.

Year	Troop Size	Residents			Newcomers		Disappearances				Total[1]	Food supply[2]
		Male		Female	Male	Female	Male		Female			
		N	Non				N	Non	N	NON		
1971	96	6	6	36	6 (2)	-	12 (10)	1	9 (8)	-	27 (23	
1972	105	6	11 (1)	41	11	-	15 (11)	11	10 (7)	-	37 (19)	197
1973	93	4	11	42	6	-	6 (4)	2	6 (6)	-	15 (11)	228
1974	109	4	15	48	16 (1)	2	15 (14)	14 (1)	28 (18)	2	61 (36)	112
1975	91	4	17	40	5	-	13 (11)	9	18 (10)	-	40 (21)	57
1976	74	2	13	33	4	-	7 (6)	8 (1)	10 (7)	-	27 (16)	83
1977	65	2	9	31	1	-	6 (5)	3	17 (8)	-	29 (15)	74
Total	633	28	82 (1)	271	49 (4)	2	74 (61)	68 (2)	98 (64)	2	236 (141)	

Figures in parentheses indicate animals of four and less than four years old.
N: natal animals; Non: non-natal animals
[1]Including infants whose sex was unknown (see table 1, FUKUDA, 1988)
[2]Cal. per capida per diem

Among troop animals at least 5 years of age, including residents and newcomers, there was a significant correlation between the number of males and females in each year ($r_s = 0.922$, N = 7, df = 5, p < 0.05; primiparous age was confirmed from 5 years of age: cf. FUKUDA, 1988, Table 1), irrespective of the amount of artificial food supply (Table 4). The existence of such a correlation suggests that the number of males at least 5 years old was affected by the number of females at least the same age. The number of non-natal or natal males was also affected by the number of females, and the values for the three age-sex groups were closely associated with one another.

Seven Types of Males after Natal Dispersal
During the seven-years between April 1971 and March 1978, 49 non-natal males and 2 non-natal females were observed in T troop, and another 6 non-natal males were known to have been in it before April 1971 (FUKUDA, 1988). Of these 55 non-natal males, 19 (34.5 %) came from adjacent troops: P (n = 14), P1 (n = 1), H (n = 3), and S (n = 1). Most of the non-natal males were at least 5 years old (n = 51), and all of the young males 4 years of age or less (n = 4) originated in adjacent troops. Five to 6 and 10 to 11 year old males were most common among the newcomer males when

first seen in T troop. Younger males, less than 9years old, tended to stay continuously for more than three years, while about half of the males at least 9 years of age tended to leave and join T troop repeatedly over a period of a year or more. Such leaving and joining males, when they were not seen in the subject troop, were usually found in adjacent troops (FUKUDA, 1982). Thus, 10 to 31 non-natal males were always observed in T troop each year, comprising more than 80 % of the males age 5 or older in the troop.

Those 55 non-natal males were classified into seven types on the basis of their association with other troop-members and their range (Fig. 4). *Waiting type* (n=8): males foraged in their own small ranges overlapping with the range of T troop. This type copulated with females foraging in their range during the mating season. In the non-mating season, these males were in friendly contact with other members of the
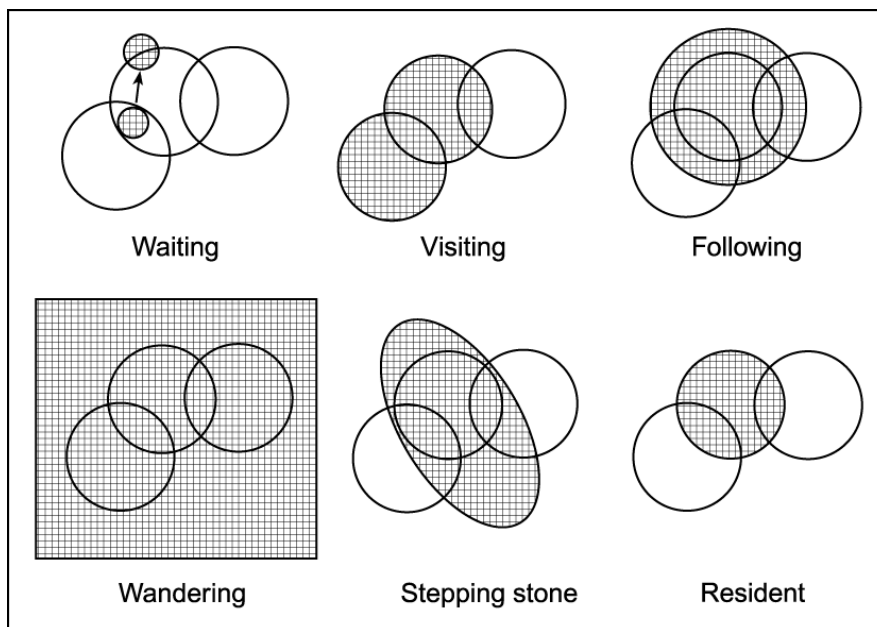
Fig. 4: Six types of male ranges after natal dispersal.
Circle= range of troop. Shadow= range of male.

troop. *Following type* (n=15): males often followed T troop. They frequently formed all-male groups and small-sized groups including females (cf. FUKUDA, 1989). Their ranges were somewhat larger than the ranges of T troop. *Wandering type* (n=5): males wandered from one troop to another and mated with females of each troop. When such males were not seen in T troop, they were seen in an adjacent troop. The range of a "wandering type" encompassed the whole Hakone area. *Visiting type* (n=5): these males were higher ranking males of their troops, but in the mating season they frequently left their troops to mate with females of adjacent troops. These males deserted their troops completely after one or more mating sea-

sons. *Resident type* (n=13): these males were higher-ranking males in the troop and mated with only females of the troop, and their ranges coincided with that of the troop. *Stepping stone* type (n=7): these males were sometimes seen only in T troop for a few years irrespective of season, and they were never chased out by females and/or resident males. If these males dispersed to other troops, they repeated the same "stepping stone" pattern. Their ranges were larger than their troop's range. *Passing type* (n=12): these males were sometimes seen in or near the troop for only a few days to some months, and, thereafter, were never seen in or near the troop again. Perhaps they went out of the Hakone area. Thirteen non-natal males became "resident type" males, among them, 6 were "resident types" from the beginning, 6 turned into the "resident type" from the "following type", and the remaining one was initially the "waiting type."

These facts suggest that, after natal dispersal, male Japanese macaques have various flexible foraging and mating strategies ("alternative behavioral phenotypes" or "alternative reproductive behaviors"), and there is a high possibility that, after natal dispersal, males form a new troop comprising female deserters and/or their offspring. In particular, a "resident type" male has the possibility of forming a new troop with female deserters (cf. FUKUDA, 1991, 1992).

We confirmed 115 natal males born in T troop over a 13 year period from 1965 to March 1978 (animals which were born in 1965 were censused in the next year). Among these males, 97 (84.3 %) have disappeared from the troop. Twenty-five (25.8 %) of these disappeared natal males were confirmed after disappearance (21 males emigrated into other troops, 2 were captured, and 2 died). The age when these 21 males deserted from T troop ranged from 2 to 7 years of age. Among 21 deserters, 18 were found in adjacent troops (P troop: n= 12, P2: n= 1, H: n= 3, S: n= 2), and 3 were found in the Hagachi troop, about 60 km south from the center of the range of T troop. One 4-year old who was in T troop in March 1978 deserted from the troop in August 1980 and was found in the Hagachi troop in December 1981 (FUKUDA, 1982).

Among all disappearances for the 15 years from 1966 to 1981, including non-natal males from T troop, only three tattooed males were found alive outside the Hakone area. In the neighborhood of the Hakone area, macaque troops inhabit the central and southern part of the Izu peninsula, the Tanzawa Mountains, and Mount Ashitaka (Fig. 1). Among 97 disappearing natal males of T troop, 49 disappeared before they were 2 years of age. These disappearing males were thought to be dead since male macaques less than 2 years old rarely survive on their own. Out of the remaining 48 disappearances of natal males 2 years of age or more, 18 (37.5 %) were found alive in the Hakone area, 3 were found in another area, but the remaining 28 (58.3 %) were not found again. Many of them probably dispersed into other areas including the Izu Peninsula, Mount Ashitaka, or the Tanzawa Mountains, such as the three tattooed males.

It is unlikely that all disappearing males died. Feral dogs probably represented the only predator for them. However, in Japan, if feral dogs are found, they are captured by public officers. Tourists sometimes fed the monkeys along the roads in the Hakone area. As a result, there is a high possibility that some macaques from T troop were killed in traffic accidents. On the other hand, macaques sometimes raid orchards during the winter season, and some of the monkeys from this study were

most likely captured or shot (cf. FUKUDA, 1988). However, if they were killed, shot, or captured, this information is easily retrievable from the department of Wildlife Conservation and Management of the Kanagawa prefecture government. To date, we have not obtained this information about our study animals.

There is a high possibility that many males dispersed into areas other than Hakone because the Hakone area is located only about 20 km to the west of the Tanzawa mountains which is inhabited by some troops of *M. fuscata*. Accordingly, most newcomer males originating from unknown troops are thought to originate from the Tanzawa, the Izu, and other areas. Although there is a highway between the Hakone and the Tanzawa areas, wild animals can move under the road. Irrespective of some highways between the Hakone and Izu areas, three dispersing males from T troop crossed them and transferred into the Hagachi troop located in the southern part of Izu Peninsula. KAWAMOTO (1997, 2002) clarified the distribution of mitochondria DNA (mtDNA) of Japanese monkeys in Kantou-Koushinetsu district (see Fig. 5). This suggests that even females may disperse to areas other than Hakone. The Hakone area probably plays a role as a corridor between the Tanzawa and Izu areas.
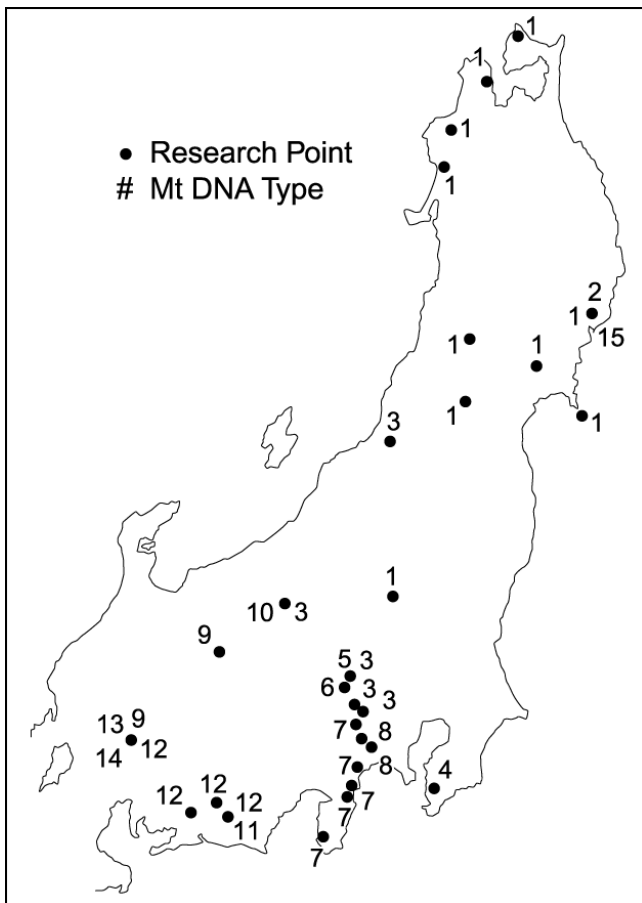

Fig. 5: The distribution of mtDNA variation of Japanese macaques in eastern Japan (after KAWAMOTO, 1997, Fig. 2). Dots indicate sites of data collection. Numbers indicate mtDNA type. Hagachi, Hakone, and Tanzawa results are of the same mtDNA type (type 7).

The Present Situation of the Hakone Area and the Meaning of Female Dispersal

The present ranges of the troops in Hakone area are shown in Fig. 6 (after MCMHWKP, 1998, Fig. 3). In Hakone area, every macaque troop moved down from the mountain area. It is suspected that one factor for the moving of their range is environmental disturbance. The total population size seems not to have decreased significantly, probably because troop members frequently invade farms and orchards and obtain high nutrient foods.
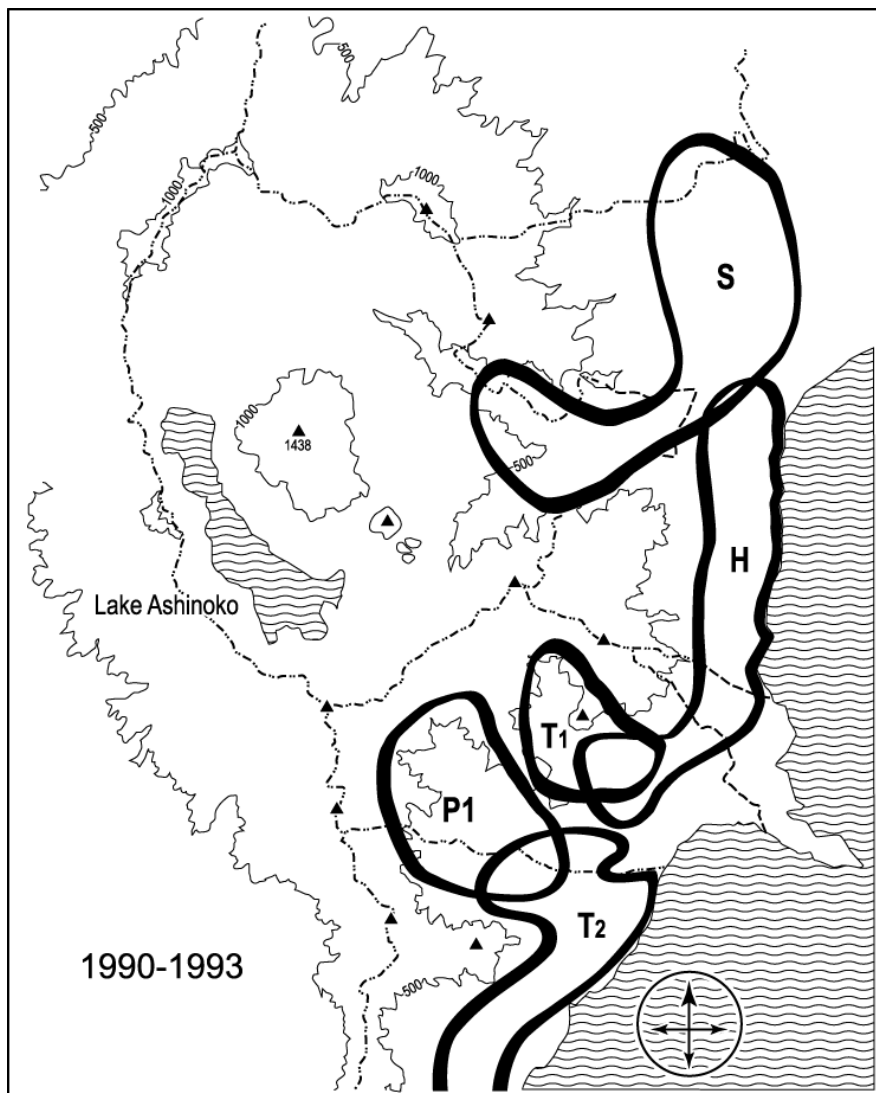
Fig. 6: Ranges of five troops (S, H, T1, T2, and P1) in the Hakone Mountains between 1990 and 1993 (redrawn from MCMHWKP, 1998, Fig. 3). Bold lines indicate each troop's range.

On the other hand, within the last half century in the Tanzawa area, two big dams, whose catchments are about 200,000,000 m^3 and 100,000,000 m^3, were constructed. Many golf courses were created, many forest roads have been cut and paved, and steep slopes along the roadside were covered with concrete. The Hakone has been similarly modified. In Japan, much of the natural destruction and exploitation of natural resources have been carried out in every part of the mountainous areas, not only of Tanzawa and Hakone Mountains. As a result, the habitat of wildlife animals, including Japanese macaques, has been destroyed and some troops of Japanese macaques have been moved from the mountainous area, although invasions to cultivated areas of these troops are also based on other artificial factors (WATANABE, 2000). Because of habitat destruction, then, female and male macaques disperse widely, including into metropolitan areas. It is quite apparent that the appearances of male and female macaques within the city limits are caused by the shortage of natural food resources resulting from the destruction of their habitat.

Environmental Disturbance and the Origin of Pioneers

When habitat is destroyed and/or the environment becomes severe, macaques disperse not only into adjacent areas but also distant regions. In these conditions, males and females disperse from their troops. Four hundred thousand years ago, the ancestors of Japanese macaques migrated from the southern part of the Korean peninsula into the northern part of Kyushu district of Japan when Japan and Korea were connected during the glacial epoch of the Pleistocene (MITO and WATANABE, 1999). The ancestors of Japanese macaques crossed the corridor into the Kyushu district, settling there. Exhibiting characteristics of populations in the early stage of growth, they gradually expanded their habitats (distribution) when environmental circumstances were good, that is, when sufficient food was available for these monkeys, and were able to broaden their range into habitat unoccupied previously by macaques, rapidly increasing their population. Because of an abundant supply of food, the primiparaous age was probably younger than at the present time, rates of conception and birth rates were probably high, infant mortality and death rates were probably low, natal males tended to stay in their natal troops, new troops were formed by troop fission, etc. (FUKUDA, 1988, 1992). During the glacial epoch, however, there were fluctuating periods of good and severe environmental circumstances (MITO and WATANABE, 1999).

Based upon knowledge of dispersal patterns under present conditions of environmental disturbance, I speculate that the expansion of the Japanese macaque's distribution would have occurred as follows. When the environment was good, their distribution enlarged gradually by means of troop-fission; however, when the environment was severe, females as well as males deserted from their troops and dispersed into distant rather than adjacent areas. As a result, the distribution of Japanese macaques enlarged rapidly and widely. By the latter process, they reached the Shimokita Peninsula, the most northern area presently inhabited by *M. fuscata*. There is a possibility, therefore, that the macaques distributed in the Shimokita Peninsula have many characters of the ancestors of Japanese macaques, as described by FUKUDA (1992).

It is possible that such a dispersal strategy in conditions of severe environmental disturbance, as above-mentioned, would be general to mammals. In times of the gla-

cial epoch, various mammals, including human beings, migrated to the American continents from Asia, crossing the Beringia (YOSHIZAKI and NYUUI, 1980). Animals would evolve so that they dispersed into more distant and more accommodating areas when the environment in one locale became severe.

References

ENOMOTO, T.: On social preference in sexual behavior of Japanese monkeys (*Macaca fuscata*). J. Hum. Evol. (1978) 7: 283-293.

FUKUDA, F.: Relationship between age and troop shifting in male Japanese monkeys. Jap. J. Ecol. (1982) 32: 491-498 (in Japanese with English synopsis).

FUKUDA, F.: Troop desertion by female Japanese macaques. Jap. J. Ecol. (1983) 33: 347-355 (in Japanese with English synopsis).

FUKUDA, F.: Influence of artificial food supply on population parameters and dispersal in the Hakone T troop of Japanese macaques. Primates (1988) 29(4): 477-492.

FUKUDA, F.: Habitual fission-fusion and social organization of the Hakone troop of Japanese macaques in Kanagawa prefecture, Japan. Int. J. Primatol. (1989) 10(5): 419-439.

FUKUDA, F.: Various ranging and mating types in male Japanese macaques after natal dispersal. In: EHARA, A., KIMURA, T., TAKENAKA, O. and IWAMOTO, M. (eds.): Primatology Today. New York: Elsevier Science Publishers B.V. (Biomedical Division) (1991): 215-216.

FUKUDA, F.: Japanese Monkeys in the Mt. Hakone. Tokyo: Shobunsha (1992) (in Japanese).

FUKUDA, F., TANAKA, S. and MURAMATSU, M.: Japanese monkeys in the Hakone mountains, 1. nature of the monkey gatherings. Nihonzaru (1974) 1: 63-122 (in Japanese with English summary).

FURUYA, Y.: On the fission of troops of Japanese monkeys: 1. Five fissions and social changes between 1955 and 1966 in the Gagyuzan troop. Primates (1968) 9: 323-350.

ITANI, J.: Social structure of primates. Ecological course 2. Tokyo: Kyoritsu-shuppan (1972) (in Japanese).

KAWAMOTO, Y.: Genetic monitoring of the local population of Japanese macaques using mitochondrial DNA variations. Wildlife Forum (1997) 3 (1): 31-38 (in Japanese).

KAWAI, M.: Ecology of Japanese Monkeys. Tokyo: Kawadeshobou-shinsha (1969) (in Japanese).

KAWAI, M., AZUMA, S. and YOSHIBA, K.: Ecological studies of reproduction in Japanese monkeys (*Macaca fuscata*). Primates (1967) 8: 35-74.

KAWAMOTO, Y.: Genetic diversity of Japanese macaque populations in the Kanto – Koshinetsu districts. Wildlife Forum (1998) 4 (2): 53-55 (in Japanese).

KOYAMA, N.: Changes in dominance rank and division of a wild Japanese monkey troop in Arashiyama. Primates (1970) 11: 335-390.

MELNICK, D.J. and PEARL, M.C.: Cercopithecines in multimale groups: Genetic diversity and population structure. In: SMUTS, B.B., CHENEY, D.L., SEYFARTH, R.M., WRANGHAM, R.W. and STRUHSAKER, T.T. (eds.): Primate Societies. Chicago: The University of Chicago Press (1987): 121-134.

MITO, Y. and WATANABE, K.: History of Japanese Macaques with Men. Tokyo: Tokai University Press (1999) (in Japanese).

MORI, A.: Analysis of population changes y measurement of body weight in the Koshima troop of Japanese monkeys. Primates (1979) 20: 371-397.

OI, T.: Sociological study on the troop fission of wild Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island. Primates (1988) 29: 1-19.

PUSEY, A.E. and PACKER, C.: Dispersal and philopatry. In: SMUTS, B.B., CHENEY, D.L., SEYFARTH, R.M., WRANGHAM, R.W. and STRUHSAKER, T.T. (eds.): Primate Societies. Chicago: The University of Chicago Press (1987): 250-267.

SUGIYAMA, Y.: On the division of a natural troop of Japanese monkeys at Takasakiyama. Primates (1960) 2: 109-148.

SUGIYAMA, Y.: Population dynamics of Japanese macaques at Ryozenyama, 3: female desertion of the troop. Primates (1982) 23: 31-44.

TAKAHATA, Y.: The socio-sexual behavior of Japanese monkeys. Z. Tierpsychol. (1982) 59: 89-108.

THE MANAGEMENT COMMITTEE OF MONKEYS HOME IN THE WESTERN KANAGAWA PREFECTURE (MCMHWKP).: The Research Report of Wild Japanese Monkeys. Yokohama: Kanagawa-ken (1998) (in Japanese).

WATANABE, K.: Crop-raiding by Japanese Macaques and Wildlife Management. Tokyo: Tokai University Press (2000) (in Japanese).

YOSHIZAKI, S. and NYUUI, Y.: The Plain Beringia Disappeared. Tokyo: NHK Books (1980) (in Japanese).

Correspondence to:
Dr. Fumio Fukuda D.Sc., 2-27-12, Shonandai, Fujisawa, Kanagawa252-0804 JA-PAN. E-mail: fukuda.fumio@jcom.home.ne.jp; TBC01727@nifty.ne.jp

THE BIOGEOGRAPHICAL EVOLUTION AND PHYLOGENY OF THE GENUS *PRESBYTIS*. MEIJAARD, E. AND GROVES, C.P.

Key words: primate, biogeography, craniometrics, phylogeny, *Presbytis*, metachromism, distribution, South-East Asia, Sundaland

Abstract

The genus *Presbytis* is more or less confined to Sundaland, and, within this region, the distribution of its species is partly a result of changes in geography, sea levels, and vegetation during the Pleistocene (and perhaps of the Late Pliocene) and partly of present-day soils and vegetation. We use the molecular cladogram of ZAIN, the phylogenetic insights of BRANDON-JONES, and our own craniometric analysis to elucidate the past patterns of vicariance, dispersal, and range contraction and expansion.

Introduction

In this paper, we examine the biogeography of *Presbytis*, a genus of leaf monkey (Colobinae) confined to Sundaland, i.e., the Malay peninsula (including peninsular Thailand) and the western Indo-Malay archipelago (Sumatra, Java, Borneo, the Natuna Islands, the Riau Islands, and the Mentawai Islands) (see Figure 1). Although in the seminal work of NAPIER and NAPIER (1967) leaf monkeys now belonging to other genera were placed in the genus *Presbytis* and only five species (*P. aygula, P. melalophos, P. frontatus* [sic], *P. rubicundus* [sic] and *P. potenziani*) were recognized in the group now under consideration, the group has become more and more speciose as understanding has grown. GROVES (2001) has produced a working taxonomy (here reproduced as far as is necessary in Table 1) with explanations of how it differs from those of earlier authors, in particular, the important contributions of BRANDON-JONES (1977, 1996a,b,c, 1998) and AIMI and his colleagues (AIMI and BAKAR, 1996; AIMI et al., 1986), as follows:

- Sumatran/Malay peninsular *P. femoralis* is now universally regarded as a species distinct from *P. melalophos*.
- BRANDON-JONES (op.cit.) has recognized *P. siamensis* as a further Sumatra/ Malay species.
- GROVES (2001) separates Bornean *P. chrysomelas* from *P. femoralis.*
- The species formerly called *Presbytis aygula* [a name which does not in fact refer to a leaf monkey but to a macaque (NAPIER and GROVES, 1983)] has been broken up. POCOCK (1935), AIMI and BAKAR (1996) and GROVES (1970) have separated Sumatran *P. thomasi* and Bornean *P. hosei* from Javan *P. comata*. BRANDON-JONES (1996b) did not recognize this separation, and continued to refer all three to a single species, *Presbytis comata.*
- On the other hand, BRANDON-JONES (1995) separated *P. fredericae* from *P. comata* as a distinct species; NIJMAN (1997), however, showed that the two grade insensibly into each other over a wide area.

We may mention that work on the genus continues, and it is far from certain that the number of valid species is at a maximum; in particular, we are of the opinion that *P. hosei sabana* and *P. h. canicrus* should be regarded as separate species from *P. hosei*.
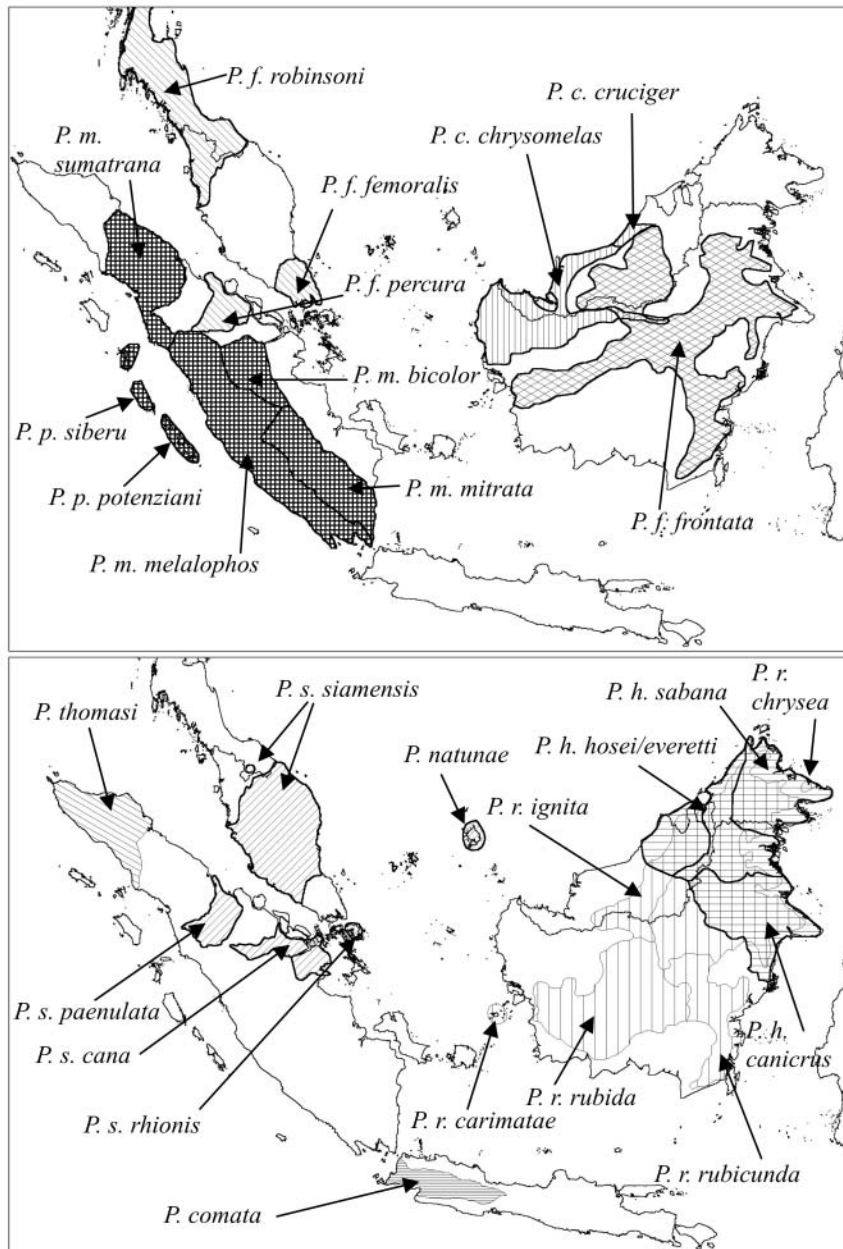

Fig. 1: Distribution of *Presbytis* species, according to GROVES' (2001) taxonomy.

Table 1: Post-1977 Taxonomic Arrangements of the Genus *Presbytis*.

GROVES, 2001	BRANDON-JONES, 1977, 1996a, b, c	AIMI et al., 1986; AIMI and BAKAR, 1996	Distribution
P. melalophos melalophos			W. Sumatra
P. m. bicolor			C. Sumatra
P. m. sumatrana			N.W. Sumatra, Batu Is.
P. m. mitrata			S. Sumatra
P. femoralis femoralis			Johor
P. f. robinsoni			N. Malay peninsula
P. f. percura			E.C. Sumatra
P. natunae			Bunguran I.
P. chrysomelas (2 subspp.)	Subspp. of *P. femoralis*		N. coast Borneo
P. siamensis siamensis		Subspp. of *P. femoralis*	Peninsular Malaysia
P. s. rhionis			Bintang I.
P. s. cana			Kundur I., E.C. Sumatra
P. s. paenulata			E.C. Sumatra
P. frontata			C. & E.Borneo
P. comata comata			W. Java
P. comata fredericae	Distinct sp.		C. Java
P. thomasi	Subspp. of *P. comata*		Far N. Sumatra
P. hosei hosei			N.E. Sarawak coast
P. h. everetti			Inland Sarawak, W. Sabah
P. h. sabana			Sabah
P. h. canicrus			E. Kalimantan
P. rubicunda (6 subspp.)			Borneo, Karimata Is.
P. potenziani (2 subspp.)			Mentawai Is.

Phylogenetic Relationships

   BRANDON-JONES (1977) proposed a set of evolutionary relationships among *Presbytis* species based mostly on coat coloration (Figure 2a). He suggested that the most primitive form of *Presbytis* is *P. potenziani* from the Mentawai Islands, off western Sumatra, with dark coloration, followed by the intermediate forms, *comata*,

thomasi, and *hosei* (which he united in a single species, *P. comata*), and culminating in the most derived forms, *P. melalophos*, *femoralis*, *frontata*, and *rubicunda*, with red/brown coloration. Among the "derived" forms, BRANDON-JONES (1996b) proposed a special affinity between *P. melalophos* and *P. rubicunda* because of similarities in behavior. Based on head pattern, BRANDON-JONES further proposed that *P. rubicunda* derived from *P. siamensis*. He also suggested a close evolutionary affinity between *P. frontata* and *P. comata sabana*, based on shared external cephalic structures. BRANDON-JONES (1996c) provided the following hypothesis for the evolution of *Presbytis comata*: During the late Middle Pleistocene the species was continuously distributed across Borneo and Sumatra. *Presbytis* was initially contracted to the Mentawai Islands by a severe glaciation at 190 thousand years (Kyr) ago. At this time, neither the Mentawai endemic *P. potenziani* nor its descendant *P. comata* had colonized Borneo, and *P. comata* evolved from *P. potenziani* after this glacial period. The next glacial period restricted *P. comata* to several glacial refugia, including one in north Borneo, in approximately the same area as the present-day distribution range of what he referred to as *P. comata everetti* (i.e., western Sabah and eastern Sarawak). The three peripheral Bornean subspecies of *P. comata* (*hosei*, *canicrus*, and *sabana*) appear to represent the first stage of extra-refugial dispersal. BRANDON-JONES also hypothesized a glacial refugium in northern Sumatra, from which populations dispersed. One branch (*P. melalophos*) dispersed as far as the southern tip of the island, and another emigrated to the Malay Peninsula and northwest Borneo. The only possible instance of sympatry resulted from a reverse dispersal of *P. siamensis* from the Malay Peninsula (BRANDON-JONES, 1996c). To allow for the interstadial dispersal from Sumatra to Borneo, BRANDON-JONES hypothesized an eastward current that carried rafts of floating vegetation between the two islands.

Melding BRANDON-JONES's model of color evolution with the principle of metachromism of HERSHKOVITZ (1967; 1977), GROVES (1989) proposed a centrifugal speciation hypothesis for the genus. He saw black – gray – red/brown as increasingly centrally evolved and dispersing out to replace the more plesiomorphic colors, so that the primitive black *P. potenziani* remains only on the Mentawai Islands, the grey *P. comata*, *P. thomasi*, and *P. hosei* are in Java, northern Sumatra and northeastern Borneo, respectively. The remaining species, all red or brown, are central in distribution (spoiling this is a tendency for the apomorphic ones to revert to black in some areas: *P. melalophos sumatrana, P. femoralis chrysomelas*).

AIMI and colleagues (AIMI and BAKAR, 1996; AIMI et al., 1986) considered the taxonomy of the genus in Sumatra, recognizing three species distinguished alike by characters of pelage, skull and vocalization. In this model, *P. melalophos* is the sister species to a clade containing *P. femoralis* plus *P. thomasi*. They effectively completed the metachromatic progression by describing a new subspecies, *P. melalophos bicolor*, the whitest, and so, in the Hershkovitzean scheme, most apomorphic of all in the central Sumatran highlands.

ZAIN (2001) used various molecular techniques, including mtDNA markers (ND3, ND4L, ND4, and tRNAs), paternal Y-chromosome markers (TSPY and SRY), and biparental autosomal markers (IRBP intron-3), to investigate phylogenetic relationships among several (but not all) *Presbytis* species (Figure 2b). He also used the DIVA program (see RONQUIST, 1997) to reconstruct the possible ancestral distri-
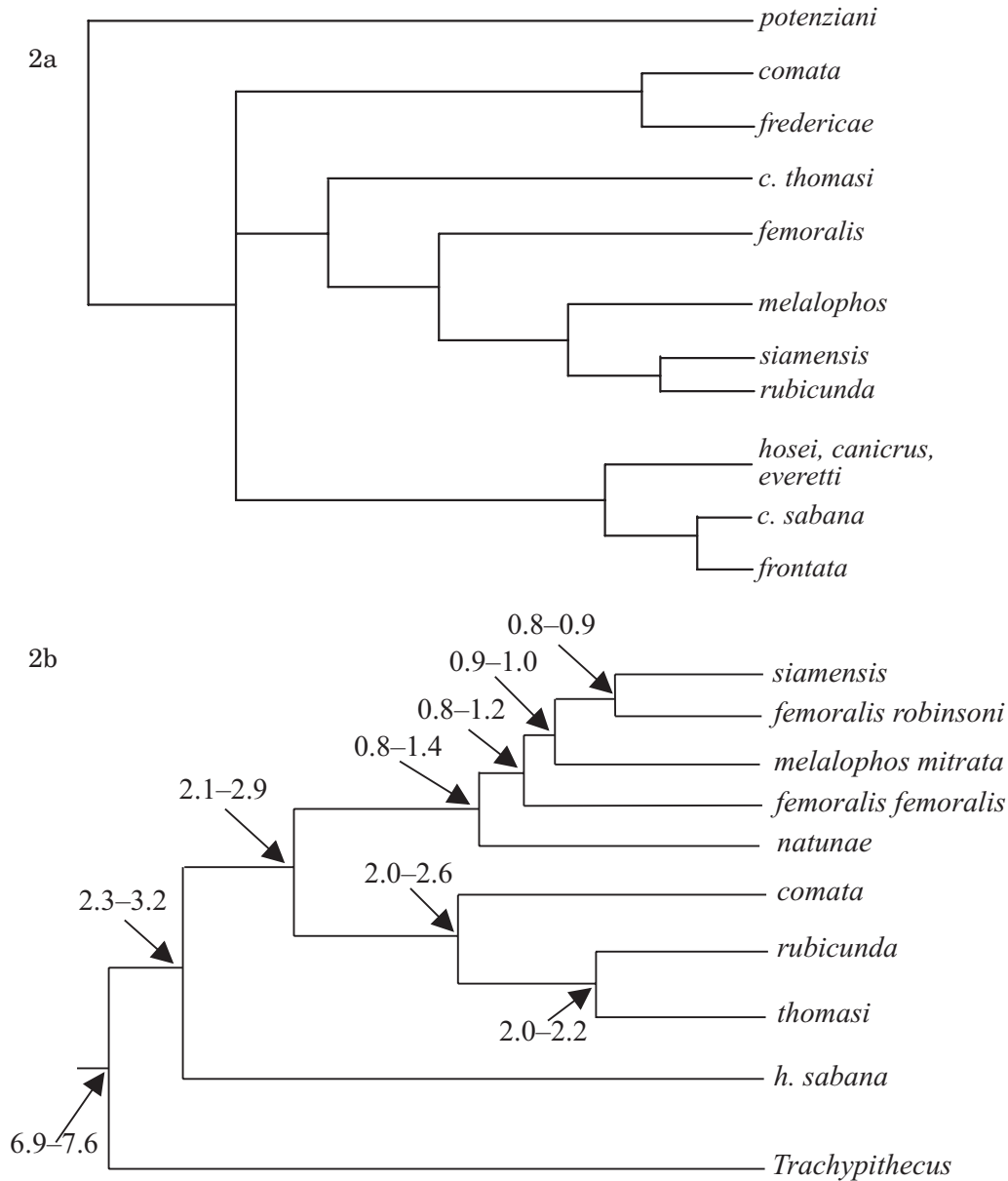
Fig. 2: Phylogeny of Presbytis, after (a) BRANDON-JONES, 1996a,b, and (b) ZAIN, 2001. Note that, strictly speaking, BRANDON-JONES regards some living taxa as unchanged ancestors of others, but in (a) they have here been represented as sister taxa for comparison with ZAIN's phylogeny. In (b), the subspecific names used by ZAIN have where appropriate been changed to specific names as in Table 1 and in the text. Numbers in (b) refer to estimated divergence times between clades [after Fig. 3.10 in ZAIN (2001)]. Taxa not included in this research were: *femoralis percura*, Sumatran *siamensis* subspp., *frontata*, *potenziani*, *h.hosei* and *everetti*, and *canicrus*.

bution of the genus *Presbytis*. ZAIN's main conclusions, relevant to this research, were that:

- *P. comata*, *P. thomasi*, and *P. hosei* are separate entities and do not belong to the same species as suggested by CHASEN (1940), HOOIJER (1962), and recently restated by BRANDON-JONES (1996a).
- *P. rubicunda* and *P. melalophos* (including *P. siamensis*) are not closely related. Instead, *P. rubicunda* groups closely with a clade containing *P. thomasi* and *P. comata*, a result that is strongly supported by high bootstrap values.
- The ancestral *Presbytis* underwent two cladogenic events on Borneo. The first split separated into *hosei* and a clade containing all other *Presbytis*. This second clade underwent a further cladogenic subdivision into a *melalophos*-like group and a *comata/thomasi/rubicunda* clade.

The chain of evolutionary events suggested by ZAIN (2001) involves a dispersal pattern starting on Borneo, moving west to the Malay Peninsula and Sumatra, and south to Java. This is exactly opposite to the direction of events proposed by BRANDON-JONES (1996a), whose ancestral species moved from the Mentawai Islands to the east via Sumatra [note, however, that ZAIN (2001) did not study *P. potenziani* from the Mentawai Islands]. ZAIN (2001) estimated that the divergence time among *Presbytis* species ranged from 3.2 to 0.8 Ma; although, *P. potenziani* was probably the species that first diverged from the other *Presbytis* (BRANDON-JONES, 1996a, and also see below), and *Presbytis* evolution thus started earlier.

One of us (EM) has investigated the palaeoenvironments of the SE Asian region in the Late Tertiary to Late Quaternary (MEIJAARD, 2003a) and has also worked extensively on the distribution of Bornean primates (e.g., MEIJAARD and NIJMAN, 2000; MEIJAARD and NIJMAN, 2003). Furthermore, we statistically analyzed measurements on 277 colobine skulls which provided additional insight into the phylogenetic relationships within *Presbytis*. These craniometric data will be published elsewhere. In this paper, we use our palaeoenvironmental reconstructions and combine them with our latest biogeographic and taxonomic insights to test which of the above biogeographical scenarios is more parsimonious with our data.

Palaeoenvironmental reconstructions

ZHANG et al. (1993) suggested that Asian colobines migrated into Sundaland during the Late Pliocene or Early Pleistocene; the earlier part of the time span fits the divergence times estimated by ZAIN (2001). They migrated from Africa to India and dispersed into southern India, Burma, Malaya and Sundaland. It is possible that, at the same time, another migratory route existed along the northern bank of the Tethys Sea in southern Tibet via Yunnan into Vietnam and, finally, toward the east around the Sichuan Basin. For colobines, that may have meant that there were two important centers of radiation, one being Sundaland and the other being the Heng Duan mountain region (ZHANG et al., 1993). The split between *Nasalis* and *Presbytis* occurred approximately 5 Myr ago, according to SARICH (1970), after which *Simias* and *Nasalis* split. ZAIN (2001), however, estimated an earlier split, 6.7–7.4 Myr ago, between *Nasalis* and *Presbytis*, based on a cercopithecine-colobine divergence of 10-11 Myr [DELSON, personal communication, quoted in ZAIN

(2001)]. Presumably, this split occurred in Sundaland, whereas the mainland Asian colobines diverged in the other center of radiation (ZHANG et al., 1993).

If the *Presbytis* group, indeed, entered Sundaland at the end of the Miocene or in the Early Pliocene, they would have followed a route along the Malay Peninsula into what is now Borneo, and possibly Sumatra (see below). Java became disconnected from this landmass after the Early Pliocene, and dispersal to Java could only have occurred across sea water (Figures 3 and 4). The proto-Kapuas River could have been a barrier between the northern and southern part of Sundaland, although no evidence concerning this is presently available.
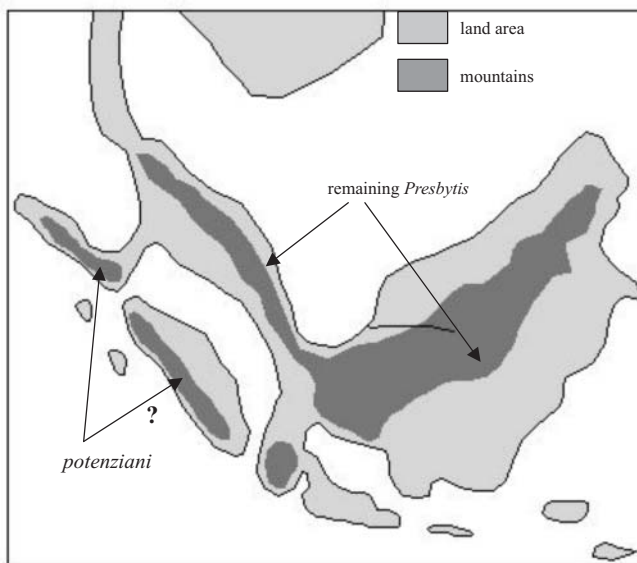

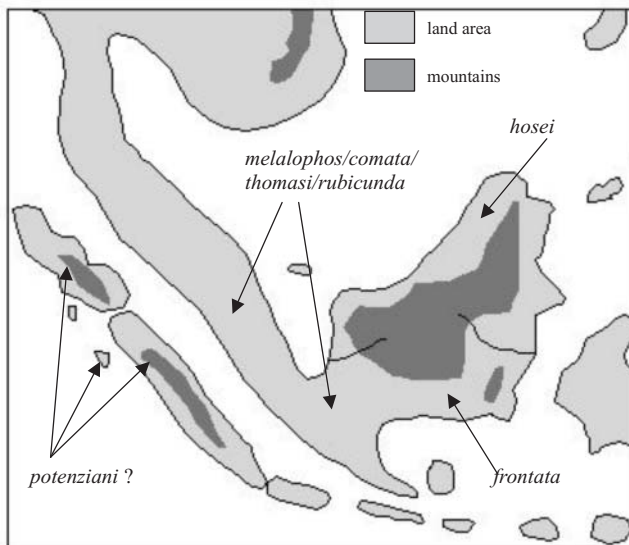Fig. 3: Land distribution during the Late Miocene–Early Pliocene.

Fig. 4: Land distribution in the Late Pliocene–Early Pleistocene.

A land connection between Borneo and western Java probably existed in the Late Miocene-Early Pliocene (ca. 7–5 Myr ago) (MEIJAARD, 2003a), but it is unlikely that leaf monkeys had already entered Sundaland at that time. The first time that *Presbytis* monkeys could have migrated to Java would have been in the Early–Middle Pleistocene, as is also suggested by fossil finds of *Presbytis aygula* (=*comata*) (HOOIJER, 1962) and other similar-sized monkeys of the genera *Macaca* and *Trachypithecus* [e.g., van den BERGH, 1999; JABLONSKI and TYLER, 1999; but note that LARICK et al. (2000), suggested that this happened much later, in the Middle–Late Pleistocene]. This land connection between Borneo/Malaya and Java probably disappeared after the Middle Pleistocene (see van BEMMELEN, 1970), which would have isolated the species on Java. The arrival of a new Late Pleistocene fauna on Java as shown in the fossils of the Punung fissures (e.g., BADOUX, 1959) indicated that by approximately 80–60 Kyr ago Java had once more become connected to the rest of Sundaland. It is unclear whether this fauna originated from Borneo or from Sumatra, or from both, but the species composition (including *Capricornis sumatraensis*, *Hylobates syndactylus*, *Elephas maximus*, and *Sus scrofa vittatus*) strongly suggests a land link between Sumatra and Java. All of these species now occur in Sumatra but not in Borneo; *Elephas maximus* is thought to be a recent arrival on Borneo (MEDWAY, 1977).

It is unclear for how long Sumatra remained an island. The Asahan Arch, a land bridge between the Malay Peninsula and northern Sumatra (see Figure 3), may have existed until the Late Miocene or Early Pliocene (MEIJAARD, 2003a), but it is unclear whether this predated the arrival of *Presbytis* in Sundaland or not. It could be that *Presbytis* arrived on Sumatra as early as the Late Miocene–Early Pliocene, and did not survive (see below), whereas "modern" species arrived on Sumatra only during the Middle–Late or Late Pleistocene, presumably when a land connection with the Malay Peninsula and Java was established. There are also indications that northern Sumatra remained an island separate from southern Sumatra during much of the Pleistocene (MEIJAARD, 2003a), and, possibly, *P. thomasi* evolved on this isolated northern island.

The Mentawai Islands probably became sub-aerial in the Pliocene (see SAMUEL et al., 1997), when the island arc was uplifted. Presumably, this led to increased sedimentation in the seas between the islands and the mainland, and it is unclear whether and when the islands were connected to Sumatra. Siberut, Sipura, and the Pagai Islands are presently all separated from Sumatra by seas < 100 m deep, and it is therefore likely that low sea-levels during the Late Pleistocene would have connected the islands to the mainland. This is also indicated by the mammalian faunas on these islands which appear to be a mixture of endemic species and ones that are much more widespread in Sundaland (e.g., MEIJAARD, 2003b). Still, the relative paucity of common Sundaland species in the southern Mentawai Islands suggests that if a last glacial maximum (LGM) land connection existed between these islands and mainland Sumatra, it probably still posed a considerable ecological barrier, limiting the dispersal of terrestrial mammals to and from these islands.

The question of when Borneo first became an island is of considerable importance to the evolution of leaf monkeys. Borneo had for a very long time been part of the Asian mainland through its connection with the Malay Peninsula. LLOYD (1978 cited in WILSON and MOSS, 1999) suggested that Borneo lost its connection to the

mainland during the latest Miocene or Pliocene, which was possibly caused by global sea-level changes and/or plate readjustments (WILSON and MOSS, 1999), but EM's reconstruction indicates that this may have happened later. Also, because the seas between Borneo and Malaya would probably have been shallow, they would have been greatly influenced by glacially induced sea-level changes.

Fossil record

The fossil record for the colobines in island South-East Asia is relatively poor. On Java, HOOIJER (1962) tentatively identified some Middle Pleistocene remains as *Presbytis*, which he considered to be identical to *P. aygula* (= *P. comata*). On Borneo, there is a relatively large sample of cranio-dental remains from the Niah Cave area in north-east Sarawak. According to HARRISON (2000) this material, which dates back to the Late Pleistocene, definitely does not include *P. femoralis* (= *P. chryso-melas*), and is most similar to *P. rubicunda* and *P. hosei*. The colobines from Gua Sireh, a Holocene deposit in western Sarawak, appear to be assignable to a single species of *Presbytis*, which is presumably *P. chrysomelas* (HARRISON, 2000). In Sumatra, HOOIJER (1962) described *Presbytis* remains from the Late Pleistocene cave deposits of Lida Air in Central Sumatra, but he could not determine their specific identity.

Phylogenetic reconstruction based on craniometrics

In addition to the data by BRANDON-JONES (1996a, b) and ZAIN (2001), we obtained further phylogenetic data by statistically analyzing measurements on 277 colobine skulls including all the *Presbytis* species and *Trachypithecus cristatus* and *T. obscurus* as outgroups (MEIJAARD and GROVES, unpublished data). First, we obtained unstandardized canonical discriminant functions evaluated at group means, which provided the input in a dissimilarity matrix based on the square root of the squared Euclidean distance between species. Dendrograms were constructed using MEGA version 2.1 (KUMAR et al., 2001). The resulting Neighbour-Joining tree, rooted at the split between *Trachypithecus* and *Presbytis* (Figure 5), indicated
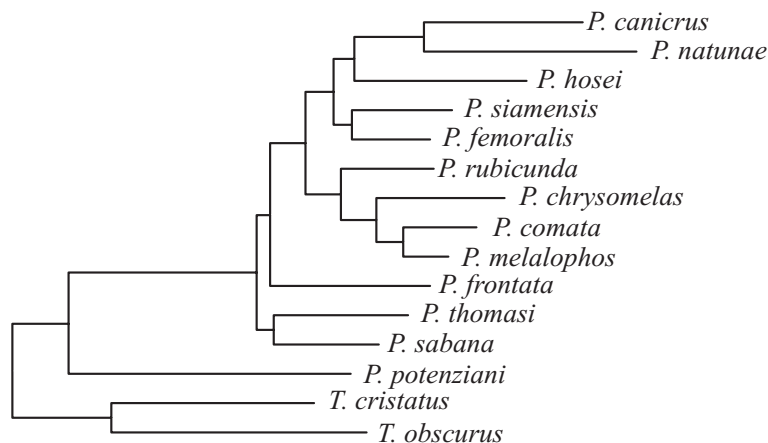

Fig. 5: Phylogenetic tree based on craniometrical dissimilarities between *Presbytis* species (MEIJAARD and GROVES, unpublished data).

that initially *P. potenziani* and the other *Presbytis* diverged, which is in accordance with BRANDON-JONES [1999, note that ZAIN (2001) did not include *potenziani* in his analysis]. From this point onwards, our phylogenetic reconstruction deviates from that of BRANDON-JONES by splitting a clade containing *sabana* (but not *hosei* and *canicrus*) and *thomasi* from the other *Presbytis*. Interestingly, ZAIN, who only used samples from *sabana* and not other taxa in the in *hosei* group, also proposed an early divergence of *sabana* (note, however, that we only measured 2 *sabana* skulls and that the early split of this species does not have statistically significant support). Our data also support the earlier mentioned hypothesis that *canicrus* should be considered a species distinct from *hosei* and *sabana*, which is primarily based on the significantly longer palate in *canicrus* together with a relatively short cranium.

Discussion

Based on the existing information, we attempt to reconstruct how leaf monkeys could have dispersed through and evolved in the region. It appears that they initially arrived from the Asian mainland probably sometime during the Late Miocene–Pliocene. Considering the early divergence of *potenziani*, hypothesized by BRANDON-JONES and supported by our craniometric data, the ancestral *potenziani* probably entered Sumatra across the Asahan Arch (Figure 3), which shortly afterwards became submerged, cutting off connections between Malaya/Borneo and Sumatra. *P. potenziani* evolved on Sumatra and spread to the Mentawai Islands during the Pliocene–Pleistocene. Why the species became extinct on mainland Sumatra is unclear. It may either have been displaced by a later *Presbytis* species, or, maybe, its habitat temporarily disappeared during one of the many Pleistocene glacials. None of the phylogenetic reconstructions supports a sister species relationship between *potenziani* and *thomasi*, although WILSON and WILSON (1977), who compared *Presbytis* vocalizations, suggested that the two may be subspecifically related. Still, it is unlikely that *potenziani* and *thomasi* arose vicariantly when the Mentawai Islands and Sumatra became disconnected.

In Borneo/Malaya, several million years later, a split probably occurred between *sabana* (with or without the other species from the *hosei*-group) and *frontata*. We hypothesize that this split happened at the start of the Pleistocene and was caused by the development of the Mahakam River. SMIT-SIBINGA (1953) stated that, ca. 2 Myr ago, the Mahakam River came into being, because of uplift in the central Borneo region, and that this river initially flowed into the very large Kutai Lake (of which the present lakes are only remnants). Together with the Kapuas River in west Borneo, this could have divided Borneo into 2 distinct regions.

Sometime during the Pliocene or Pleistocene the separation of Borneo from the Malay Peninsula would have provided a mechanism for the divergence between the *siamensis/femoralis/melalophos/chrysomelas* group and the remaining Bornean *Presbytis* species. *P. comata* would subsequently have migrated to Java across an Early–Middle Pleistocene land bridge, but it is unclear whether this land bridge was only connected to the Malay Peninsula or whether there was also a direct link to Borneo. ZAIN's (2001) data and our craniometrical analysis support a close relationship between the Javan *comata* and the Bornean *rubicunda*. Although there is limited

concordance between the 3 phylogenetic models regarding the relationships between *thomasi*, *comata*, and *rubicunda*, ZAIN's data strongly suggest that the 3 species form a monophyletic clade. We speculate that an ancestral species on the southern Malay Peninsula, or on the peninsula's extension along the Riau/Lingga Archipelagos and Bangka and Belitung Islands, crossed to Sumatra, Java, and Borneo during an Early-Middle Pleistocene glacial period. It remains unclear where and for how long these land connections between Malaya, Java, Sumatra, and Borneo existed. During the Early–Middle Pleistocene, the following situation may have existed:

- In northern Borneo, the *hosei*-group occurred, separated by the Kapuas and Mahakam Rivers from the *frontata*-ancestor.
- In southwest Borneo, *rubicunda* lived.
- On Java, *comata* occurred.
- On most of Sumatra, *thomasi*—*potenziani* having by then been isolated on the Mentawai Islands, whereas the *melalophos*-group (including *siamensis*, *femoralis*, and *natunae*) occurred on the Malay Peninsula and its southern extension to the Riau, Lingga, Bangka, and Belitung areas (see Figure 6).
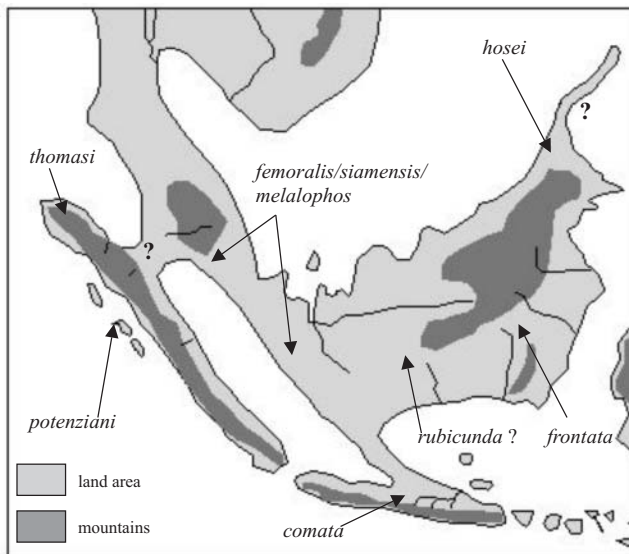

Fig. 6: Land distribution during an Early–Middle Pleistocene period of low sea-levels.

Assuming that ZAIN's (2001) divergence times are approximately correct, speciation in the *melalophos*-group happened during the Middle Pleistocene, sometime between 1.4 and 0.8 Myr ago. Van den BERGH et al. (1996) suggested that a regime of moderate sea-level fluctuation mode had existed since 2.4 Myr BP but that this changed dramatically to high amplitude fluctuations during the Middle–Late Pleistocene (app. 800 Kyr ago). Minimum sea levels dropped to 170 meter below the present-day levels. These much lower sea-levels could have provided opportunities for dispersal of the *melalophos*-group into Borneo and Sumatra, which, after sea-levels rose, would have isolated them in those areas (Figure 7).
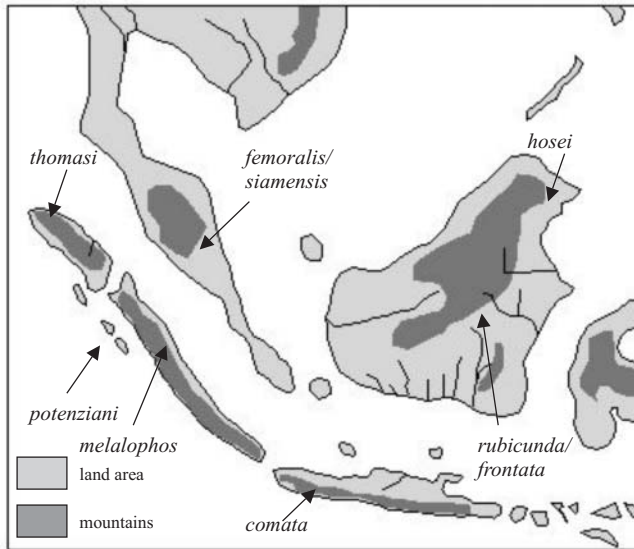
Fig. 7: Land distribution during a Middle Pleistocene period of high sea-levels.

The 3 phylogenetic models do not agree on the relationships between *melalophos*, *femoralis*, *siamensis*, and *natunae*, and the speciation model for this group remains unclear. Considering that *melalophos* occurs exclusively on Sumatra, evidently its evolution was the direct result of the dispersal of its ancestor from Malaya to Sumatra during a period of low sea-levels, after which it was isolated again when sea-levels rose. On Sumatra, *melalophos* would have encountered *thomasi*, unless the latter species was already isolated in north Sumatra (north of the Sibolga area), which EM thinks may have been an island for much of the Pleistocene.

Interestingly, ZAIN (2001) estimated that *natunae* diverged from the rest of the *melalophos*-group between 1.4 and 0.8 Myr ago, which suggests that its ancestor dispersed from Malaya to the Bunguran Island area (to which *natunae* is now restricted) or that it evolved elsewhere as an isolated population, before being restricted to the Bunguran Island area after the LGM. We do not have an explanation for the divergence between *femoralis* and *siamensis*, which presumably occurred on the Malay Peninsula and its southern extension. During periods of low sea-level, large rivers may have dissected this narrow land area, especially in the more eroded southern parts (where now only small island groups remain), and possibly the two species became isolated by one of these rivers.

Having provided a working model for speciation within *Presbytis*, we will now try to find an explanation for some of the peculiar distribution patterns, and the subspeciation within the group. Firstly, there is the unusual situation of general sympatry between the Bornean species (Figure 1, Table 2): *P. rubicunda* is sympatric with each of the others, and locally there is marginal sympatry between pairs of others, whereas on Sumatra and in Malaysia, the species occur almost completely allopatrically. BRANDON-JONES (1996b) ascribed this to different climatic histories of Pleistocene refugia in the two islands. We suggest that it relates, rather, to present-day ecology.

Table 2: Sympatric Species of Two Dietary Guilds in Borneo and Sumatra.

Borneo		
folivores/granivores Colobines		**frugivores Cercopithecine + Hylobatids**
N. Kalimantan and E. Sarawak	**Sabah; W. Sarawak + most of Kalimantan**	
N. larvatus	*N. larvatus*	*Macaca fascicularis*
P. rubicunda	*P. rubicunda*	*M. nemestrina*
P. hosei or *canicrus*	*P. sabana* or *frontata* or *chrysomelas*	*Hylobates muelleri* or *albibarbis*
P. frontata or *chrysomelas*	*T. cristatus*	
T. cristatus		
Sumatra		
Presbytis sp.		*M. fascicularis*
T. cristatus		*M. nemestrina*
		H. lar or *agilis*
		Symphalangus syndactylus

The higher population density (and correlated behavioral differences) of orang-utans (*Pongo* spp.) in Sumatra compared to Borneo has been interpreted as springing from Sumatra's greater soil fertility, and consequent higher biotic productivity (DELGADO and van SCHAIK, 2000). In Africa, trees in forests growing on poor soils have leaves with highly developed toxic defenses against predation, and the arboreal primates that are most diverse and most abundant are those able to detoxify them, such as many colobines. It is in such forests that specialized leaf eaters and seed predators (e.g., most *Presbytis*) predominate in the poorest soils of all. On the other hand, on better soils, there is a greater diversity of trees with fleshy fruits, and all monkey taxa are more frugivorous than their vicariants in regions of poorer soil. In the richer regions of West-Central Africa, colobines, primarily folivorous, are absent altogether, with the exception of *Colobus guereza*, which at Makokou is actually predominantly a frugivore (GAUTIER-HION, 1984; GAUTIER-HION et al., 1985).

Dipterocarps form an even higher proportion of the canopy in Borneo than in Sumatra, Borneo or Java (WHITMORE, 1975, especially pp.182-185). The fact that *hosei, sabana*, and *canicrus* occur sympatrically with *rubicunda*, and partly with *frontata* and *chrysomelas*, and *rubicunda* is sympatric with each of the others, suggests that there are three ecologically distinct groups. MITCHELL (1994) suggested that where *hosei* (that is, the species from the *P. hosei* group) is sympatric with *rubicunda*, the former may be found more often in the upper canopy and emergents of a forest while *rubicunda* is more often found lower down. *P. hosei* is primarily folivorous (MITCHELL, 1994; RODMAN, 1978), whereas *rubicunda* is mixed granivorous, frugivorous, and folivorous (DAVIES, 1984), or even mostly seed or fruit eating (van SCHAIK et al., 1992). Such considerable ecological differences indicate that the species are also genetically rather distinct, an assumption which is supported by ZAIN's (2001) data. We therefore hypothesize that the poorer soils of Bor-

neo have permitted colobines to specialize in narrow feeding niches, where they experience limited competition from their closest relatives. On Sumatra, on the other hand, there is ecological scope for only a single folivore-granivore specialist, there is considerable competition for the same resources, and species tend to remain allopatric. Clearly, this hypothesis requires further testing.

Further, unusual distribution patterns that require an explanation are found in Sumatra. Firstly, it is remarkable that *Presbytis* is absent from Bangka and Belitung, and the south-east coast of Sumatra, although a large number of other tropical forest species occur in these areas. MEIJAARD (2003b) found evidence that, during the LGM, several areas in Sundaland were too dry to retain a closed forest cover (see Figure 8). Although EM found no such evidence for the Bangka, Belitung, and south-east Sumatra areas, others (e.g., HEANEY, 1991, see Figure 8) have included these areas in the dry zone. This could explain why *Presbytis* species did not occur in these 3 areas during the LGM, and we hypothesize that they did not manage to re-invade after climatic conditions improved.
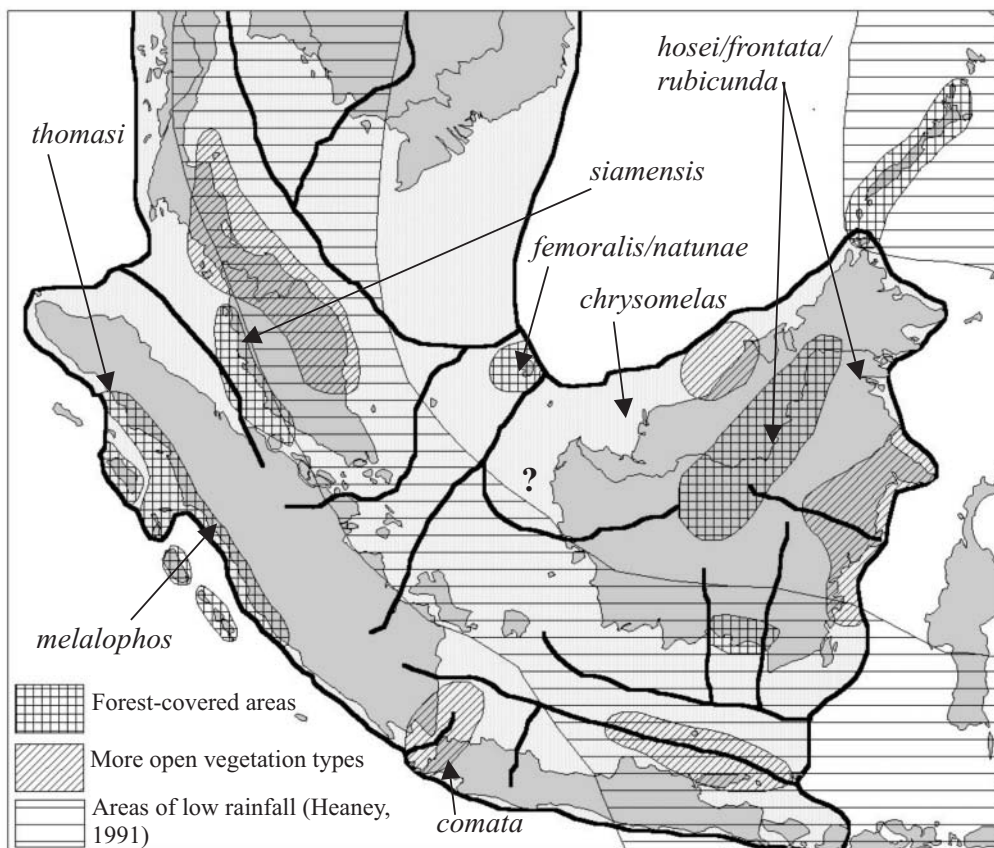

Fig. 8: Land distribution during the Last Glacial Maximum, including wet and dry zones (after MEIJAARD, 2003b).

Figure 8 also provides an explanation for the curious distribution patterns of *P. f. percura*, *P. s. paenulata*, and *P. s. cana* (see Figure 1). Because of the existence of drier vegetation types during the LGM that were unsuitable for *Presbytis*, species would have retreated into wet forest refugia. Figure 8 shows that such refugia existed near the mouth of the Molengraaff River (hereafter named Bunguran refugium) and on the west side of the mountains of Malaya (west Malay refugium). MEIJAARD's hypothesis is supported by CRANBROOK (2000), who stated that "the faunal list from 40+ Kyr in Sarawak does not support BRANDON-JONES's (1998) postulate that, from 80 Ka, conditions of cold and aridity eliminated forest habitat suitable for leaf monkeys and orangutans". CRANBROOK does, however, suggest that, during the LGM, lower montane forest could have vegetated the entire present lowland area of Borneo, as indicated by the fossil finds at sea-level of montane mammals such as Lesser Gymnure (*Hylomys suillus*) and Ferret Badger (*Melogale personata*). If such temperature sensitivity is a key factor, then for long periods during the LGM, the rich flora of the lowland mixed dipterocarp forest formations must have been confined to extreme lowland elevations, perhaps in river valley refugia or on the maritime periphery. On good soils, forest patches could have attained high stature. There must have been a variety of evergreen trees, with a sufficiently extended fruiting season, to support large frugivore primates (orang-utan), as well as a perennial leaf cover to feed the folivorous leaf monkeys.

If we assume that *femoralis* retreated to the Bunguran refugium, and *siamensis* to the west Malay one, then after the climatic amelioration, when sea-levels started to rise, *femoralis* could have migrated west following the courses of the main rivers, which would have led them northwest towards central Malaya and southern Thailand, and west-southwest towards their present-day Sumatran ranges. *P. siamensis*, on the other hand, could have stayed in the west Malay refugium, but presumably found an opportunity to reach eastern Sumatra, directly opposite its Malayan range. *P. femoralis*, on its return to Sumatra, drove a wedge in the *siamensis* population. ZAIN's (2001) data show that this may not be the full story, as he found that *P. femoralis femoralis* and *P. f. robinsoni* diverged during the Middle Pleistocene, ca. 750 Kyr before the LGM, while also suggesting that *femoralis* is not monophyletic relative to *melalophos* and *siamensis*. This could mean that *P. f. robinsoni*, from the northern Malay Peninsula, is specifically distinct from *P. femoralis femoralis* and *P. f. percura*. Further taxonomic and phylogenetic work is needed before we can really test the above hypothesis.

For *P. chrysomelas*, a similar scenario can be developed, with the species retreating towards the Bunguran refugium during the LGM (note that there are no pre-Holocene fossils of this species on mainland Borneo), after which it reinvaded Borneo from the west. *P. chrysomelas* largely displaces both *frontata* and *rubicunda* in the lowlands of Sarawak (BANKS, 1931; NIJMAN and MEIJAARD, in preparation), whereas in east Borneo, where *chrysomelas* is absent, *frontata* and *rubicunda* are found at low elevations. This suggests that *chrysomelas* occupied the exposed Sunda Shelf during the LGM, and when sea-levels started to rise it moved into western Borneo, thereby displacing *frontata* and *rubicunda*, especially in swamp areas.

Conclusion

In this paper we have attempted to merge information from a variety of sources, including genetics, morphological studies, and palaeoenvironmental reconstructions, to improve our understanding of the evolution of *Presbytis* leaf monkeys in the Sundaic Region. We think that our model is in general agreement with the existing data, although many hiatuses remain in our knowledge. Further work is needed on the phylogeny of the genus, especially addressing *potenziani*, *frontata*, the *hosei*-group, and *chrysomelas*, while also more research is needed to provide more accurate palaeoenvironmental maps.

Acknowledgements

References

AIMI, M. and BAKAR, A.: Distribution and deployment of *Presbytis melalophos* group in Sumatra, Indonesia. Primates (1996) 37: 399-409.

AIMI, M., HARDJASASMITA, H.S., SJARMIDI, A. and YURI, D.: Geographical distribution of Aygula-group of the genus *Presbytis* in Sumatra. Kyoto University Overseas Research Report of Studies on Asian Non-Human Primates (1986) 5: 45-58.

BADOUX, D.M.: Fossil Mammals From Two Fissure Deposits at Punung (Java); With Some Remarks on Migration and Evolution of Mammals During the Quaternary in South-East Asia. Utrecht, The Netherlands: Rijksuniversiteit Utrecht (1959).

BANKS, E.: A popular account of the mammals of Borneo. Journal of the Malayan Branch of the Asiatic Society (1931) 9: 1-137.

BEMMELEN, van R.W.: The Geology of Indonesia. General Geology of Indonesia and Adjacent Archipelagoes (2nd Edition), Vol. 1A. The Hague, The Netherlands: Martinus Nijhoff (1970).

BERGH van den, G.D.: The Late Neogene Elephantoid-Bearing Faunas of Indonesia and Their Palaeozoogeographic Implications. A Study of the Terrestrial Faunal Succession of Sulawesi, Flores and Java, Including Evidence for Early Hominid Dispersal East of Wallace's Line. Leiden, The Netherlands: National Natuuhistorisch Museum (1999).

BERGH van den, G.D., DE VOS, J., SONDAAR, P.Y. and AZIZ, F.: Pleistocene zoogeographic evolution of Java (Indonesia) and glacio-eustatic sea level fluctuations: a background for the presence of Homo. Bulletin Indo-Pacific Prehistory Association (1996) 14: 7-21.

BRANDON-JONES, D.: The evolution of recent Asian colobines. In: CHIVERS, D.J. and JOYSEY, K.A. (eds.): Recent Advances in Primatology. London: Academic Press (1977): 323-325.

BRANDON-JONES, D.: *Presbytis fredericae* (Sody, 1930), an endangered colobine species endemic to Central Java. Primate Conservation (1995)16: 68-70.

BRANDON-JONES, D.: The Asian Colobinae as indicators of Quaternary climatic change. Biological Journal of the Linnean Society (1996a) 59: 327-350.

BRANDON-JONES, D.: *Presbytis* species in sympatry in Borneo versus allopatry in Sumatra: an interpretation. In: EDWARDS, D.S.E.A. (ed.): Tropical Rainforest Research - Current Issues. Dordrecht, The Netherlands: Kluwer Academic Publishers (1996b): 71-76.

BRANDON-JONES, D.: The zoogeography of sexual dichromatism in the Bornean grizzled sureli, *Presbytis comata* (Desmarest, 1822). Sarawak Museum Journal (1996c) 5: 177-200.

BRANDON-JONES, D.: Pre-glacial Bornean primate impoverishment and Wallace's line. In HALL, R. and HOLLOWAY, J.D. (eds.): Biogeography and Geological Evolution of SE Asia. Leiden, The Netherlands: Backhuys Publishers (1998): 393-404.

CHASEN, F.N.: A handlist of Malaysian mammals. a systematic list of the mammals of the Malay Peninsula, Sumatra, Borneo and Java, including the adjacent small islands. Bulletin of the Raffles Museum, Singapore, Strait Settlements (1940) 15: 1-209.

CRANBROOK, EARL OF.: Northern Borneo environments of the past 40,000 years: Archaeozoological evidence. The Sarawak Museum Journal (2000) 55: 61-109.

DAVIES, A.G.: An Ecological Study of the Red Leaf Monkey (*Presbytis rubicunda*) in Dipterocarp Forest of Northern Borneo. Cambridge, UK: University of Cambridge (1984).

DELGADO, R.A. and van SCHAIK, C.P.: The behavioral ecology and conservation of the orangutan (*Pongo pygmaeus*): a tale of two islands. Evol. Anthropol. (2000) 9: 201-218.

GAUTIER-HION, A.: Seed dispersal by African forest cercopithecines. La Terre et la Vie: Revue d'Ecologie Appliquee (1984) 39: 159-166.

GAUTIER-HION, A., DUPLANTIER, J.-M., QURIS, R., FEER, F., SOURD, C., DECOUX, J.-P., DUBOST, G., EMMONS, L., ERARD, C., HECKETWEILER, P., MOUNGAZI, A., ROUSSILHON, C. and THIOLLAY, J.-M.: Fruit characteristics as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia (1985) 65: 324-337.

GROVES, C.P.: The forgotten leaf-eaters, and the phylogeny of the Colobinae. In: NAPIER, J.R. and NAPIER, P.H. (eds.): Old World Monkeys. Evolution, Systematics, and Behaviour. New York and London: Academic Press (1970): 555-588.

GROVES, C.P.: A Theory of Human and Primate Evolution. Oxford: Clarendon Press (1989).

GROVES, C.P.: Primate Taxonomy. Washington DC, U.S.A.: Smithsonian Institution Press (2001).

HARRISON, T.: Archaeological and ecological implications of the primate fauna from prehistoric sites in Borneo. Indo-Pacific Prehistory Association Bulletin (2000) 20: 133-146.

HEANEY, L.R.: A synopsis of climatic and vegetational change in Southeast Asia. Climatic Change (1991) 19: 53-61.

HERSHKOVITZ, P.: Metacromism or the principle of evolutionary change in mammalian tegumentary colors. Evolution (1967) 22: 556-575.

HERSHKOVITZ, P.: Living New World Primates (Platyrrhini), With An Introduction to Primates. Vol. 1. Chicago and London: The University of Chicago Press (1977).

HOOIJER, D.A.: Quaternary langurs and macaques from the Malay archipelago. Zoologische Verhandelingen, uitgegeven door het Rijksmuseum van Natuurlijke Historie te Leiden (1962) 55: 1-64.

JABLONSKI, N.G. and TYLER, D.E.: *Trachypithecus auratus sangiranensis*, a new fossil monkey from Sangiran, central Java, Indonesia. Int. J. Primatol. (1999) 20: 319-326.

KUMAR, S., TAMURA, K., JAKOBSEN, I.B. and NEI, M.: MEGA2; molecular evolutionary genetics analysis software. Bioinformatics (2001) 17: 1244-1245.

LARICK, R., CIOCHON, R.L., ZAIM, Y., SUDIJONO, SUMINTO, RIZAL, Y. and AZIZ, F.: Lithographic context for Kln-1993.05-SNJ, a fossil colobine maxilla from Jokotingkir, Sangiran Dome. Int. J. Primatol. (2000) 21: 731-759.

MEDWAY, LORD: Mammals of Borneo. Monographs of the Malaysian Branch of the Royal Asiatic Society (1977) 7: i–172.

MEIJAARD, E.: Solving mammalian riddles. a multi-disciplinary reconstruction of the Tertiary and Quaternary distribution and dispersal and dispersal of selected mammals and their palaeoenvironments in Sundaland and Wallacea. PhD dissertation. Department of Anthropology and Archaeology, Canberra, Australia: Australian National University (2003a).

MEIJAARD, E.: Mammals of Southeast Asian islands and their Late Pleistoene environments. Journal of Biogeography (2003b) 30(8): 1245-1257.

MEIJAARD, E. and NIJMAN, V.: Distribution and conservation of the proboscis monkey (*Nasalis larvatus*) in Kalimantan, Indonesia. Biol. Conser. (2000) 92: 15-24.

MEIJAARD, E. and NIJMAN, V.: Primate hotspots on Borneo: predictive value for general biodiversity and the effects of taxonomy. Conser. Biol. (2003): 725-732.

MITCHELL, A.H.: Ecology of Hose's langur, *Prebytis hosei*, in mixed logged and unlogged Dipterocarp forest in north Borneo. Ph.D. Dissertation, Yale University, New Haven, CT, U.S.A. (1994).

NAPIER, P.H. and GROVES, C.P.: *Simia fascicularis* Raffles, 1821 (Mammalia, Primates): request for the suppression under the plenary powers of *Simia aygula* Linnaeus, 1758, a senior synonym. Z.N.(S.) 2399. Bulletin of Zoological Nomenclature (1983) 40: 117-118.

NAPIER, J.R. and NAPIER, P.H.: Handbook of Living Primates. London: Academic Press (1967).

NIJMAN, V.: Geographical variation in pelage characteristics in *Presbytis comata*. Z. für Säugetierkunde (1997) 62: 257-264.

RODMAN, P.S.: Diets, densities, and distributions of Bornean primates. In: MONTGOMERY, G.G. (ed.): The Ecology of Arboreal Foliovores. Washington, D.C.: Smithsonian Institution Press (1978): 465-478.

RONQUIST, F.: Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. Syst. Biol. (1997) 46: 195-203.

SAMUEL, M.A., HARBURY, N.A., BAKRI, A., BANNER, F.T. and HARTONO, L.: A new stratigraphy for the islands of the Sumatran Forearc, Indonesia. Journal of Asian Earth Sciences (1997) 15: 339-380.

SARICH, V.M.: Primate systematics with special reference to old world monkeys. a protein perspective. In NAPIER, J.R. and NAPIER, P.H. (eds.): Old World Monkeys: Evolution, Systematics, and Behaviour. New York and London: Academic Press (1970):175-226.

SCHAIK van, C.P., ASSINK, P.S. and SALAFSKY, N.: Territorial behavior in Southeast Asian langurs: resource defense or mate defense? Am. J. Primatol. (1992) 26: 233-242.

SMIT-SIBINGA, G.L.: Pleistocene eustasy and glacial chronology in Borneo. Geologie en Mijnbouw (1953) 15: 121-136.

WILSON, C.C. and WILSON, W.L.: Behavioral and morphological variation among primate populations in Sumatra. Yearb. Phys. Anthropol. (1977) 20: 207-223.

WILSON, M.E.J. and MOSS, S.J.: Cenozoic palaeographic evolution of Sulawesi and Borneo. Palaeogeography, Palaeoclimatology, Palaeoecology (1999)145: 303-337.

ZAIN, B.M.: Molecular systematics of the genus *Presbytis*. Unpublished PhD Dissertation. New York: Columbia University (2001).

ZHANG, Y.P., LIANG, R.P. and JABLONSKI, N.G.: Classification and evolution of Asian colobines. Folia Primatol. (1993) 60: 106-117.

Correspondence to:
Dr. Erik Meijaard, School of Archaeology and Anthropology, Faculty of Arts, A.D. Hope Building, Australian National University, Canberra, ACT 0200, Australia. E-mail: erik.meijaard@anu.edu.au

BOOK REVIEW: CONCEPTUALIZING THE CAUSES OF DISPERSAL. <u>BERN-STEIN, I.S.</u>

CLOBERT, J., DHONDT, A.A., DANCHIN, E. and NICHOLS, J.D. (eds.): Dispersal. Oxford: Oxford University Press (2001). 452 pp., $50.00.

Although most animals have a "home range", the area in which they are almost always found, there are individuals that leave their home ranges and establish new home ranges at one or more times in their lifetime. Sometimes this dispersal is limited to one sex, and sometimes is more common at certain ages, or occurs at particular times of the year, or is more likely under particular conditions. What are the specific factors that influence which individuals will disperse and when (proximal causes)? What ontogenetic factors are responsible for the timing of dispersal in an individual's lifetime? What are the functional consequences of such dispersal? What evolutionary selective pressures would have favored the patterns of dispersal that we see?

In searching for functions, there is often a desire to identify a single function, but in the Preface to the book under review, Waser warns that dispersal may not be a unitary phenomenon. The introduction also asks if there are multiple causes behind dispersal, migration, natal dispersal, and breeding dispersal, with regard to proximal mechanisms, function, and evolutionary mechanisms. The 25 chapters that follow, divided into 5 parts, deal with problems of data collection, modeling, interpretation, etc. Some are concerned with the problems of empirical data collection under field conditions; others try to obtain knowledge by logic and reason. The Rationalist approach may use elegant reasoning but is limited by the truth and adequacy of the original assumptions. Validation is attempted by trying to match the model with data from known populations. This process essentially entails looking for data to support, rather than to test, a position, and the authors acknowledge that different biological groups seem to support different models. Perhaps in trying to understand dispersal in seeds, bacteria, and animals they have conceived the problem too broadly to come up with unitary answers? Some of the mathematical models left me with a great sense of satisfaction, after I successfully followed them. Word models can be exquisite in their presentations, but the authors warn us that: "…argument usually remains purely verbal". (PERRIN and GOUDET, p.123), "…theory in this area is essentially uncoupled from empirical research…" (HANSKI, p.285), and "…the current routine use of genetic methods to 'estimate dispersal' still has weak theoretical foundations and few demonstrated successes" (ROUSSET, p.19).

It would be easy to complain that the models are simplistic, that you cannot deduce what is not already in the assumptions, etc.; but, the authors are well aware of the shortcomings and use models, in part, because there are few empirical options. There are some beautiful natural histories of particular species, some represented by chapters in this book, but the goal is to develop a universal model to explain dispersal. In my opinion, the data seem too disparate to successfully achieve this enterprise. There are far too many variables, which *could* influence dispersal, to generate

a simple model. Given enough unmeasured independent variables, one can account for any specific value of the dependent variable (dispersal). Hanski makes it quite clear that the assumptions of most models are rarely met in nature.

Primate groups do move in space over time, and there is movement of individuals between groups. Such movement surely has the potential to influence genetic exchange patterns and diversity, distribution, conservation, evolutionary processes involving cooperation and competition, and functional outcomes like "altruism". Primatologists know about some of the variation among living forms and among individuals in a population. We try to correlate such data with sex, age, ecology, individual condition, etc. Although we have some understanding of exchange patterns in some groups, we are far from inducing a general predictive theory. This book represents the state-of-the-art in knowledge of dispersal as a general phenomenon. The general theory can explain some specific instances but cannot yet make specific predictions about a new population.

I enjoyed thinking about the topics and arguments presented in this book, but I found little that helped me to better understand the animals that I know. Some of the authors cite unpublished manuscripts, some critique WEB sites that only the experts in the field will be familiar with, and some even cite e-mail addresses as their sources. This suggests a small, tight-knit community of scholars talking among themselves and essentially excludes "outsiders". An outsider like myself may enjoy the intellectual stimulation, recognize the insights and wisdom of the authors, and feel virtuous about having studied something from new perspectives, but I doubt that I will be looking things up in this book, asking students to read portions of it to better understand primates, or that I will long keep it on my bookshelf. It may be a wonderful compilation for people in this specialty area but of little value for an outsider in another specialty area, Primatology. I do know a few of the authors, but my interest in their work is peripheral to my interest in Primates. I did not find their chapters central to my interests, but I am sure that they would not find my publications central to their interests either.

Correspondence to:
Irwin S. Bernstein, Department of Psychology, University of Georgia, Athens, Georgia 30602-3013, U.S.A. E-mail: isbern@arches.uga.edu

BOOK REVIEW: MONKEYS, MOVEMENT, AND MATH: CAN QUANTITATIVE MODELS HELP OUR UNDERSTANDING OF PRIMATE DISPERSAL PATTERNS? <u>SHULTZ, S.</u>

TURCHIN, P.: Quantitative Analysis of Movement: Measuring and Modelling Population Redistribution in Plants and Animals. Sunderland: Sinauer (1998). 406 pp., $47.95.

Quantitative Analysis of Movement was written as a handbook and reference tool for those interested in applying models to animal movement. In an effort to close the gap between mathematical and field ecology, Turchin advocates the use of simple models that provide useful predictions, which, in turn, can be tested using data collected from natural populations. As dispersal focuses on changes in spatial distribution over time, the diffusion equation, and variants thereof, serves as the basis for most of the models presented. The book also gives considerable attention to individual-based models and how to scale up from patterns of movement of dispersing individuals to overall population-level trends. The obvious subjects for the majority of the models are invertebrates, for whose taxa large numbers of individuals can be trapped and marked, allowing good estimates of the distributions of dispersal distances. There are, however, several sections specifically devoted to the problems of analysing vertebrate dispersal. Some of the more simplistic approaches (e.g., corridor use in dispersal) focus more on using qualitative data patterns to describe dispersal patterns. The quantitative models of vertebrate dispersal limit themselves to questions that can be addressed using fairly crude data, such as the distribution of individuals over space and the dispersal trajectories used by individuals searching for available territories.

There are two primary obstacles for the application of these models by primatologists. The first lies in the level of math necessary to work through the equations and understand their mechanics. The preface indicates that a basic knowledge of calculus and differential equations is sufficient to work through the models. I am, by no means, a mathematician by training but have taken calculus and theoretical ecology undergraduate and postgraduate courses. I personally found the models presented in the book difficult, although not impossible, and found it necessary to spend a considerable amount of time to sort out the different model parameters and how they were to predict changes in individual- or population-level spatial distributions. The author provides an appendix that works through the derivation of the diffusion equation; yet, even by referring to this, I often could not manage to work out the progression from one model to the next. In many cases it may be unnecessary to understand the intricacies of each model as long as the assumptions are clear and one understands the terms involved. However, it remains still unsettling to take models on faith without grasping how they work or were derived.

The second major problem is the resolution of dispersal data available to most primatologists. Dispersal, by definition, concentrates on rates of expansion and spatial changes in occupancy. Because the diffusion equation is the principle model, it is

necessary to have data about changes in area and direction over a set period of time. Most primate populations that have been studied occur in relatively stable habitats, and questions about dispersal are generally focused on how individuals redistribute themselves rather than upon how the spatial distribution of a given population changes. Generally, information on primate dispersal is limited to known individuals leaving or new individuals arriving into focal study groups. Although these research conditions allow a calculation of dispersal rates, they generally do not permit the collection of a sufficient amount of data on spatial redistribution of individuals nor on the dispersal paths of individuals that have left the group.

The book does highlight a few issues relevant to primatology that have received little attention. One potential area of interest is how individuals select or choose new home ranges and/or groups when they disperse. Multiple null models are presented in the book discussing dispersal trajectories as well as how aggregation and attraction of individuals can affect dispersal patterns. Interesting questions could potentially be asked about how dispersing individuals assess potential groups based on their group size and habitat quality. Results from studies addressing these questions might be compared with results against different search models, and predictions could be derived from ideal free distribution or optimal group size models. This necessitates, of course, sufficient field observations to compare dispersal rates into and away from groups of different sizes. This may not be completely unfeasible wherever the demographic make-up of different groups allows us to interpret the number of recent migrants into or out of groups of different sizes. Additionally, the increasing prevalence of molecular techniques to assess relatedness can lead to a better understanding of dispersal patterns and trends. Recent work on genetic structure of populations (e.g., KAPPELER et al., 2002) may also allow a determination of mean and maximum dispersal distances if the genetic structure of the population is worked out over a large space. Genetic structure of populations has already been used to understand dispersal behaviour in other taxa (RICHARDSON et al., 2002). However, these techniques remain costly in both time and resources, and gathering the minimum amount of data required to test the relevant models will would necessitate considerable investment.

In sum, although this book presents a wide range of models that can be used by those studying species that disperse over small spatial scales, for primatologists, I think there is more utility in using the book to conceptualize ideas about how individuals move through their environment rather than to provide applicable models. Hopefully, as primatologists, we can identify those models which do generate predictions testable with our data, or, conversely, discover new techniques to learn more about the dispersal of individuals over space.

References

KAPPELER, P.M., WIMMER, B., ZINNER, D. and TAUTZ, D.: The hidden matrilineal structure of a solitary lemur: implications for primate social evolution. Proc. Royal Soc. Series B (2002) 269: 1755-1763.

RICHARDSON, B.J., HAYES, R.A., WHEELER, S.H. and YARDIN, M.R.: Social structures, genetic structures and dispersal strategies in an Australian rabbit (*Oryctolagus cuniculus*) populations. Behav. Ecol. Sociobiol. (2002) 51:113-121.

Correspondence to:
Dr. Susanne Shultz, Conservation Science, RSPB, The Lodge, Sandy, BEDS. SG19 2 DL, UK. E-mail: susanne.shultz@lrspb.org.uk