THE POTENTIAL FOR METACOMMUNITY EFFECTS UPON HOWLER MONKEYS

Darwin (1859) formulated the principle of "competitive exclusion" to explain the potential for coexistence between two species. In its present terms, the principle states that "...if there is no differentiation between the realized niches of two competing species, or if such differentiation is precluded by the limitations of the habitat, then one species will eliminate or exclude the other." (Begon and Mortimer, 1986). Theoretical (De Bruyn, 1980) and empirical (Connell, 1961) work has investigated the parameters of this principle, descriptions and formulations of which depend on the existence of interspecific competition for limiting resources, such as food or space.

When species are excluded by competition, "competitive release" may occur, that is, the expansion of a species' range when a competitor is eliminated (see Begon and Mortimer, 1986). In a similar fashion, changes in the distribution and abundance of a species may occur as a result of local (metapopulation) or regional (metacommunity) colonization and extinction of given species within a community (Valone and Brown, 1995; Harrison, 1994). Nee and May (1992) investigated metacommunity ("secondary") effects with a model for two competing species while decreasing the amount of

Table 1. Interspecific interactions at feeding sites by mantled howler monkeys, *Alouatta palliata* Gray. Percentages = % total sample of 27 genera.

Class, specific example(s), and common names	Focal tree species, where identified, and notes
Insecta (15%)	
Centris aethyctera, anthophorid bees	*Andira inermis* in flower producing nectar; bees interfere with howler feeding; howlers may delay feeding until after diurnal pollination peak; bees displace monkeys.
Xylocopa spp. , carpenter bees	*Gliricidia sepum* in flower; bees decrease average feeding rate of monkeys; bees interfere with howler feeding.
Trigona fulviventris, stingless bees	Tree in flower, nectar visible; bees interfere with howler feeding.
Pseudomyrmex ferruginea, acacia ants	*Acacia cornigera*. Ants and juvenile howlers eating leaves; ants displace howlers by biting or attempting to bite.
Reptilia (7%)	
Iguana iguana, *Ctenosaura similis*, iguanas	*Licania arborea*, *Spondias* spp., *Ficus ovalis*, *Enterolobium cyclocarpum*, and *Cordia alliodora*; primarily feeding on fruit; coexistence?
Aves (67%)	
Cathartes aura, *Caracara plancus*, vultures	Female howlers emit appeasement calls to vultures; vultures displace feeding young and adult female monkeys.
Buteo magnirostris, *Spizastur melanoleucus*, hawks	Hawks displace howlers and some birds (e.g., jays) from feeding sites.
Herpetotheres cachinnans, falcons	Falcons interfere with howler feeding; howlers vocalize toward falcons.
Jabiru mycteris, storks	Low flying bird, triggers coordinated howls by male howlers; storks interfere with howler feeding.
Brotogeris jubularis, *Aratinga canicularis*, parrots	In fruiting tree; interspecific feeding associations.
Eugenes fulgens, hummingbirds	*Tabebuia neochrysantha* in flower; interspecific feeding association.
Trogon spp., trogons	In fruiting tree; interspecific feeding associations
Eumomota superciliosa, *Motmotus lessoni*, motmots	*Simarouba glauca* in fruit; birds pick fruit then leave tree to feed; motmots avoid howlers.
Rhampastos spp., toucans	*Ficus ovalis* in fruit; mutual interference in context of feeding associations.
Campephilus guatemalensis, *Dryocopus lineatus*, woodpeckers	Bird calls sound like howler barks; howlers may flush insects eaten by woodpeckers; competition for space.
Chiroxiphia linearis, manakins	Feeding in fruit tree; coexistence.
Cyanocorax spp., crows, jays	*Andira inermis*, *Anacardium excelsum*, *Muntingia calabura*; howlers may displace jays, howlers may flush insects.
Campylorhynchus rufinucha, acacia wrens	*Simarouba glauca* in fruit; howlers flush insects; interspecific feeding association.
Mammalia (11%)	
Coendou mexicanum, *Dasyprocta punctata*, rodents	*Anacardium excelsum* in fruit; commensals beneath feeding tree.
Sciurus spp., squirrels	*Ficus ovalis* in fruit; howlers displace squirrels; interspecific feeding association among howlers, ctenosaurs, parrots, trogons, jays, and squirrels.

available habitat ('patch removal'). They found that patch removal may decrease the distribution and abundance of the superior competitor, while increasing the distribution and abundance (in time and space) of the inferior competitor. Of particular importance to students of conservation biology is the finding that patch removal can effect changes in the makeup of communities in remaining inhabited patches even if these very patches have experienced no 'intrinsic' changes of their own. This process is reminiscent of the 'butterfly effect' in chaos theory whereby small perturbations may lead to large effects at a distant point in space or time. Metacommunity effects, then, are expected to be nonlinear and may be difficult to predict. For this reason they deserve particular attention from conservation biologists.

Mantled howler monkeys (*Alouatta palliata* Gray) belong to frugivore and herbivore guilds throughout their wide distribution in Meso- and South America. In this note I provide evidence of interspecific interactions between howlers and 27 other genera recorded at Hacienda La Pacifica, Cañas, Guanacaste, Costa Rica. *Ad libitum* methods of observation were employed in addition to the 'focal tree' observational method (Jones, 1983), in which a single tree upon which howlers were known to feed, generally a tree in peak flower, fruit, or leaf flush, was observed and the interactions of all animal species recorded. Feeding rates were counted as number of mouthfulls per minute.

Table 1 presents a summary of notes on interactions between howler monkeys and individuals of 27 genera. Most of these responses took place when both howlers and one or more species were feeding or attempting to feed, usually on new leaves, fruit, or flowers; plant tissues preferred by howlers (Glander, 1981) and available primarily during the dry season, which is from November to April (see Frankie *et al.*, 1974). Observations occurred more frequently in riparian habitat than in deciduous habitat (Frankie *et al.*, 1974) during the dry season (2 x 2, $p \leq 0.2$, $\chi^2 = 5.5.$, df = 1). The presence of clumped resources of high quality favors grouping tendencies, intra and interspecifically (see Pulliam and Caraco, 1978), and Table 1 shows 15 of 27 (56%) genera apparently showing feeding associations with howlers.

Observations of pairwise displacements (interference) between howlers and contraspecifics show that howlers are frequently subordinate to species with whom they divide space, food, and time (e.g., bees). Such interactions may effectively keep howler numbers in check. Related to this, howlers appear to compete directly for space with eight (30%) species (e.g., iguanas). Such potential costs may translate into decreased feeding rates with a consequently increased chance of mortality or decreased reproductive success (Schoener, 1971).

Since environmental heterogeneity, such as patchily distributed food, may increase costs to reproduction and survival, switching to alternative behaviors such as those presented in Table 1, may be favored to avoid the costs of aggression. In particular, monkeys may switch to non-damaging responses (e.g. pairwise supplantation or interspecific feeding associations) as a function of variations in feeding rates, and the particular alternative behavior observed is expected to be a function of animal species, food type and quality, feeding group size, tree size and density, as well as feeding rates (see Schoener, 1971).

Such events govern interspecific relations within patches and may be perturbed by between patch (regional) disturbances (e.g., patch removal), including extinction. As Nee and May (1992) point out, as patch extinction rate increases, the number of coexisting species does not change in a straightforward manner. The effect upon mantled howlers of the extinction of anthophorid bees 15 km away, for example, could produce no change in population size, a decrease and possible extinction, or an increase in population size. Such unpredictability injects a degree of uncertainty or stochasticity into attempts to quantify the viability parameters of populations.

If metacommunity effects can lead to the persistence or increase of inferior competitors, what traits of mantled howlers may yield higher dispersal rates, lower patch extinction rates, or less clumping in time and space compared to the species to which they are subordinate? Mantled howlers may exhibit higher colonization rates than certain of their superiors who demonstrate greater habitat specificity. Like most primates, howlers tolerate a broad range of habitats. Further, extinction rates may be lower for howlers whose dispersion in time and space is less clumped than, for example, some birds and insects.

On the other hand, howlers may be especially vulnerable to extinction because of their membership in the frugivore guild (see Terborgh, 1986). For howlers at La Pacifica, feeding rates for fruit are more variable than for new leaves or flowers ($p \leq 0.05$, $\chi^2 = 7.11$, df = 2), and higher variations in feeding rates are found in patchier deciduous habitat ($p \leq 0.01$, $\chi^2 = 6.77$, df = 1). These observations suggest that fruit is more highly dispersed for howlers than new leaves or flowers, possibly contributing to the likelihood of inreased extinction if greater heterogeneity is correlated with increased stochasticity.

Previous reports have documented interspecific associations by howler monkeys (Glander, 1979; Rockwood and Glander, 1979; Young, 1982), but none has analyzed these groups for their significance to regional colonization and extinction. Nee and May (1992) show that competitively inferior species, such as mantled howlers and many other primate species in certain regimes, will increase in number relative to competitively

superior species where rate of colonization relative to patch extinction rate of the inferior is greater than that of the superior competitor or where the dispersion of subordinates is less clumped than that of superiors. This counterintuitive result underlines the power of modeling to identify those data (e.g., dispersal and extinction rates) required to maximize the persistence of primates in communities, and introduces a concept, the metacommunity, 'secondary' to metapopulation dynamics (Valone and Brown, 1995; Harrison, 1994) which are appropriately the major focus of primate conservation biology.

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References

Begon, M. and Mortimer, M. 1986. *Population Biology: A Unified Study of Animals and Plants*. Sinauer Associates, Inc., Sunderland, Massachusetts.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42: 710-713.

Darwin, C. R. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London.

De Bruyn, G. J. 1980. Coexistence of competitors: a simulation model. *Netherlands J. Zool.* 30: 345-368.

Frankie, G. W., Baker, H. G. and Opler, P. A. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62: 881-919.

Glander, K. E. 1979. Feeding associations between howling monkeys and basilisk lizards. *Biotropica* 11: 23-236.

Glander, K. E. 1981. Feeding patterns in mantled howling monkeys. In: *Foraging Behavior: Ecological and Psychological Aproaches*, A. Kamil and T. Sargent (eds.), pp.231-258. Garland Press, New York.

Harrison, S. 1994. Metapopulations and conservation. In: *Large-Scale Ecology and Conservation Biology*, P. J. Edwards, R. M. May and N. R. Webb (eds.), pp.111-128. Blackwell Scientific Publications, Oxford.

Jones, C. B. 1983. Do howler monkeys feed preferentially upon legume flowers at flower-opening time? *Brenesia* 21: 41-46.

Nee, S. and May, R. M. 1992. Dynamics of metapopulations: habitat destruction and comparative coexistence. *J. Anim. Ecol.* 61 37-40.

Pulliam, H. R. and Caraco, T. 1978. Living in groups: is there an optimal group size? In: *Behavioural Ecology: An Evolutionary Approach*, J. R. Krebs and N. B.Davies (eds.), pp. 122-147. Sinauer Associates, Inc., Sunderland Massachusetts.

Rockwood, L. L. and Glander, K. E. 1979. Howling monkeys and leaf-cutting ants: comparative foraging in a tropical deciduous forest. *Biotropica* 11: 1-10.

Schoener, .W. 1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* 2: 36-404.

Terborgh, J. 1986. Keystone plant resources in the tropical forest. In: *Conservation Biology:: the Science of Scarcity and Diversity*, M.E.Soulé (ed.), pp.330-344. Sinauer Associates, Inc., Sunderland, Massachusetts.

Valone, R. G. and Brown, J. H. 1995. Effects of competition, colonization, and extinction on rodent species diversity. *Science* 267: 880-883.

Young, O. P. 1982. Aggressive interaction between howler monkeys and turkey vultures: the need to thermoregulate behaviorally. *Biotropica* 14: 228-231.

DIFFERING RESPONSES TO A PREDATOR (*EIRA BARBARA*) BY *ALOUATTA* AND *CEBUS*

Here I report on an observation of mantled howling monkeys (*Alouatta palliata*) and white-faced capuchins (*Cebus capucinus*) responding to a predator, a tayra (*Eira barbara*). The observation occurred on Barro Colorado Island, Republic of Panama, during an investigation into the feeding ecology of white-faced capuchins.

On 23 September 1993, while following one of the habituated capuchin study groups (see Phillips, 1994, for a detailed description of the troops), I heard loud aggressive vocalizations from capuchins and howlers. Individual capuchins traveled toward the direction of the vocalizations. I followed them, and approximately 30 seconds later came across a tayra surrounded by five capuchins and three howlers. The howlers were clustered high in the trees; the capuchins were in the understorey, close to the tayra. All were directing threats and vocalizations to the tayra, which was on a fallen tree, approximately 2 m off the ground. One adult male capuchin approached the tayra, leaning toward it while directing threats and vocalizing. After 1.5 minutes of reciprocated threats and lunges, the tayra retreated towards the ground. The adult male capuchin followed, continuing to direct threats and lunges. At all times the capuchin maintained a distance of 2-3 m. After retreating, the tayra made no aggressive response, and continued moving away from the group. Once the tayra had left the area, the howlers and some of the capuchins remained