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Competition and coexistence in mustelid communities

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Mustelid species guilds are large but competition between mustelid species appears limited except in the genera *Martes* and *Mustela*. Several different nonequilibrium community models indicate that 2 or more *Mustela* may coexist temporarily due to different reproductive adaptations, differential predation of different prey, prey population fluctuations, and predation on *Mustela* by other predators. Long-term coexistence only occurs through local extinction and recolonization.

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1. Introduction

The family Mustelidae is large and many mustelid species guilds are larger than other carnivore guilds. For example, in northeastern North America half the native carnivore species are mustelids (Hall 1981). Though competition between mustelids has not been proven (vis-a-vis Connor & Simberloff 1979), mustelid sympatry has always been explained by size differences that reduce competition for food (Rosenzweig 1966). We find it difficult to believe that size differences alone explain the coexistence of so many mustelids, especially in the genera *Martes* and *Mustela*.

We here review examples of mustelid food competition, which appears most intense within *Martes* and *Mustela*. To understand better mustelid coexistence, we investigate model communities containing *Mustela* species. Coexistence of 2 or more *Mustela* is not easy to explain, appears dependent on many factors, and may only occur for short-term periods.

2. Competition within the Mustelidae

2.1. Otter and mink

There is diet overlap between otters (*Lutra* spp.) and minks (*Mustela vision*), but otters eat mostly fish and minks eat mammals, birds, and crayfish (Wilson 1954, Erlinge 1972, Jenkins & Harper 1980), and otters prefer lakes whereas minks prefer streams (Erlinge 1972). Diet overlap is greatest in winter when both species use limited open water (Erlinge 1972). Erlinge (1972) and Jenkins & Harper (1980) disagree whether otters and minks compete.

Differences in vision and lung capacities of otters and minks indicate they compete little. Mink vision is adapted to terrestrial hunting (Dunstone & Sinclair 1978), whereas *Lutra* probably have equivalent vision above and below water, as do Asian otters (*Amblonyx cineria*, Balliet & Schusterman 1971). Minks lack the lung capacity to hunt fish effectively in open water and therefore hunt more efficiently from shore (Dunstone & O'Conner 1979).

2.2. Skunks, badgers, and sympatric Mustelinae

Skunks (*Mephetinae*) are so omnivorous (Ewer 1973) and European badgers (*Meles meles*) so specialized (Kruuk 1978), that they probably compete little with any other mustelids. American badgers (*Taxidea taxus*) have different diets than sympatric *Mustela* (Ewer 1973). Badgers eat many more ground squirrels (*Spermophilus*) than do stoats (*M. erminea*) or long-tailed weasels (*M. frenata*). Blackfooted ferrets (*M. nigripes*) specialize on prairie dogs (*Cynomys*).

2.3. Zorilla and African weasel

The zorilla (*Ictonyx striatus*) and African weasel (*Poecilogale albunucha*) are the only South African mustelines (Rowe-Rowe 1978). Both are able to kill small mammals but the weasels are specialists on small mammals and zorillas eat a wide variety of prey, including invertebrates (Rowe-Rowe 1978). Different prey sizes and specialization versus generalization allow coexistence.

2.4. Long-tailed weasel, mink and American marten

No studies consider competition between long-tailed weasels, minks, and American marten (*Martes americana*). All prey heavily on small mammals (Rosenzweig 1966) and male long-tails, minks, and female martens are similar in size. Competition is probably limited because martens prey heavily on snowshoe hares (*Lepus americanus*), long-tails are cautious about preying on animals so large (Allen 1938), and minks prefer aquatic habitats.

2.5. Genus *Martes*

Sympatric fishers (*M. pennanti*) and American martens in Canada have large diet overlaps (Clem 1977, Raine 1981). Both hunt and capture prey almost exclusively on the ground (Powell 1981, Zielinski 1981), and both prey heavily on snowshoe hares. But martens eat more small mammals and birds and fishers eat porcupines. Martens and fishers prefer late and earlier successional forests respectively (Powell 1981).

Sympatric pine martens (*M. martes*) and beech martens (*M. foina*) in Eurasia are slightly different in build but are the same size (Anderson 1970) and have almost identical diets (Goszczynski 1976). They may have different habitat preferences (Jensen & Jensen 1970). We know of no good explanation for the large diet overlap.

Little is known of beech marten and yellow-throated marten (*M. flavigula*) competition, though yellow-throated martens are large enough to prey on small ungulates (Matjushkin 1974). Pine marten and sable (*M. zibellina*) populations fluctuated inversely in western Europe in the 19th century (Yurgenson 1956). Martens, sables and kidases (marten × sable hybrids) all prey on small mammals and birds (Yazan 1970). However, if pine martens and sables are the same species (Anderson 1970), they should have similar diets.

2.6. Genus *Mustela*

Diets of sympatric weasels (*M. nivalis*), stoats and polecats (*M. putorius*) in Europe vary with predator size but for each pair of species adjacent in size there is considerable diet overlap (Poole 1970, Brugge 1977, King 1980). All 3 species take a wide range of prey.

Stoats and long-tails in California specialize on voles (*Microtus montanus*), vary greatly in population density, and decrease in numbers during vole cycle lows (Fitzgerald 1977). Long-tails range over large areas whereas stoats prefer meadows. In Ontario stoat and long-tail diets overlap, though stoats specialize more on voles (*M. pennsylvanicus*) than do long-tails, and are better adapted as subterranean and subnivian predators because of smaller body size (Simms 1979). Stoats prefer early successional communities while long-tails have no preferences.

Simms (1979) found the clearest differences between 2 small *Mustela*, though he also found diet overlap approaching 100 % in some areas and much habitat overlap. Most authors who found similar diets for small *Mustela* explained coexistence with specializations they did not measure (Brugge 1977, Fitzgerald 1977, and others). King & Moors (1979) hypothesized that weasels and stoats coexist locally because weasels excell in exploitative competition (high reproductive rates) while stoats excell in interference competition (large size). Because weasels suffer heavy predation, Powell (1979, 1982) hypothesized that predation on *Mustela* species affects population dynamics and mediates competition.

We investigated these hypotheses using several models of communities containing 2 small *Mustela* species.

3. Small *Mustela* community models

3.1. MacArthur and Levins models

Communities containing small *Mustela* species seldom reach equilibria where most community models apply. MacArthur & Levins (1976) argued that a community of n species obeying the Lotka-Volterra equations,

$$\frac{dX_i}{dt} = r_i X_i \frac{K_i - X_i - \sum_j \alpha_{ij} K_j}{K_i} \quad (1).$$

can retain all n species of each can increase when rare (n must be small, Rosenzweig pers. comm.). Species i can increase when rare if

$$K_i > \sum_j \alpha_{ij} X_j^*$$

where X_j^* are population equilibrium values when species i is absent.

For 2 species, each will increase when rare if,

$$K_1 > \alpha_{12} X_2^* = \alpha_{12} K_2 \text{ and } K_2 > \alpha_{21} X_1^* = \alpha_{21} K_1 \quad (2).$$

If a predator population preys on all species i in some manner proportional to X_i, equations (1) for the prey species become

$$\frac{dX_i}{dt} = r_i X_i \frac{K_i - X_i - \sum_j \alpha_{ij} K_j}{K_i} - {}_pX_i$$

For 2 species, each can increase when rare if

$$K_1 > \alpha_{12} X_2^* = \frac{\alpha_{12} K_2}{1 + {}_p k_1} \text{ and } K_2 > \alpha_{21} X_1^* = \frac{\alpha_{21} K_1}{1 + {}_p k_2} \quad (3).$$

Note that equations (2) and (3) differ only by ${}_pK_i$, predation, added to the denominator. Predation lowers the threshold permitting invasion by a competitor. This implies that predation on *Mustela* species allows invasion of communities by competing *Mustela*; long-term coexistence is not implied, however.

MacArthur (1970) expanded on the Lotka-Volterra equations and found a parameter Q,

$$Q = -2 \sum_i K_i X_i^* - \sum_{ij} \alpha_{ij} X_i^* X_j^*$$

such that Q is minimized in model communities that cannot be invaded by additional competitors. If one assumes for simplicity that for 2 competitors $K_i = K_2$, $\alpha_{12} = \alpha_{21}$, and predation reduces the equilibrium values of X_1^* and X_2^* equally, then adding a predator lowers Q. This also implies that predation allows invasion by a competing *Mustela* species but again does not imply long-term coexistence.

Levins (1979) concluded from different nonequilibrium model communities that the number of competitors "coexisting on resources cannot exceed the number of resources plus the number of distinct nonlinearities" in the resource equations (p. 769). For communities with 2 *Mustela* species, this implies that prey fluctuations (vole population cycles) act as an additional resource enabling coexistence that might not be possible otherwise.

3.2. Computer simulations and matrix analyses

We developed FORTRAN programs (available on request) to model communities with cyclic (voles *Microtus*; rabbits, *Sylvilagus*) and noncyclic (mice *Peromyscus*) prey, with a small and a larger *Mustela* species (e.g. stoats, long-tails), and with and without raptors that prey on all other community members. Model parameter values were taken from the literature when possible. The programs produced realistic community population dynamics. We investigated competition by removing species and by varying model parameter values.

Competition is indicated by a negative effect by 1 species on the reproduction of another. We removed each *Mustela* from the communities to see changes in mean litter size and total reproduction over 10 years of monthly iterations. Removing the competitor caused an increase in most of the reproductive measures, and most changes were greater in the community without raptors, showing that predation on *Mustela* mediated competition.

We varied initial *Mustela* population sizes, maximum litter sizes, and predation efficiency constants one at a time and recorded ranges of these parameters over which neither *Mustela* went extinct during 10 years of monthly iterations.

We modelled the smaller *Mustela* to have higher reproduction and lower mortality than the larger during low prey populations, so it remained in the communities with smaller initial population sizes. This appeared more important than maximum litter sizes, for which the larger species had larger value ranges. The smaller *Mustela* could survive without rabbits when there were no raptors, yet the larger had to have rabbits in the community. This appeared to be an effect of rabbit low population sizes and high energy content and the larger *Mustela*'s high energy demands. Differential predation on different prey was important, as for each prey there was little or no overlap of the predation efficiency constants, despite large diet overlaps.

Parameter ranges over which the model communities retained all members were larger without raptors than with raptors. This implies that the larger, more realistic community was less stable. Community matrix analysis also implies this. Letting the 3 prey be species 1 to 3, the 2 *Mustela* species 4 and 5, and the raptors species 6, and using only the signs for the α's, the community matrices with and without raptors are

$$A = \begin{matrix} - & 0 & 0 & - & - \\ 0 & - & 0 & - & - \\ 0 & 0 & - & - & - \\ + & + & + & - & - \\ + & + & + & - & - \end{matrix} \quad \text{and} \quad A^1 = \begin{matrix} - & 0 & 0 & - & - & - \\ 0 & - & 0 & - & - & - \\ 0 & 0 & - & - & - & - \\ + & + & + & - & - & - \\ + & + & + & - & - & - \\ + & + & + & + & + & - \end{matrix}$$

These matrices represent community classes that include our model communities. The necessary and sufficient criteria for stability or stable limit cycles in these community matrices are (May 1973):
1. $\alpha_{ii} \leq 0$, for all i, 2. $\alpha_{ii} \neq 0$, for at least one i, 3. $\alpha_{ij}\,\alpha_{ji} \leq 0$ for all $i \neq j$, 4. for any sequence of 3 or more indices, $i, j, k, \ldots q, r$ (with $i \neq j \neq k \neq \ldots \neq q \neq r$), the product $\alpha_{ij}\,\alpha_{jk} \ldots \alpha_{qr}\,\alpha_{ri} = 0$, 5. determinant $\neq 0$.

The communities represented by A and A' are not necessarily stable; restrictions are necessary on α_{45}, α_{54}, α_{64}, and α_{65} to meet criteria 3 and 4. This is consistent with our simulations. If predation on *Mustela* by raptors reduces α_{54} and α_{45} to 0, A' meets criterion 3. In our simulations, raptors reduce but do not eliminate competition. If the effects of *Mustela* on raptors as prey are exactly equal and opposite to their indirect effects from reducing prey populations, A' meets criterion 4. In our simulations, this happens occasionally. Reducing competition between *Mustela* stabilizes A, but adding raptors to do this requires looking at A'.

4. Discussion

Our model analyses indicate that coexistence of more than 1 *Mustela* in a community is not a simple matter. The complexities of real communities suggest that the several modelling approaches we used were necessary to give the best understanding of *Mustela* communities.

Our models support several hypotheses for coexistence of 2 *Mustela* species: higher reproduction in a smaller species due to lower energy requirements (King & Moors 1979), slightly different predation abilities (Brugge 1977, Fitzgerald 1977, Simms 1979), prey populations that fluctuate, and predation on *Mustela* (Rosenzweig 1966, Powell 1979). However, no model indicates that coexistence will be long-term. This is

clearly seen in the ways that predation and prey fluctuations affect competition and community stability.

Predation of *Mustela* reduces competition in all model communities and makes invasion by a competing *Mustela* easier. However, matrix analyses and simulations indicate that the 6 member community is less stable than the 5 member community; matrix analyses also indicates that predation on *Mustela* may make the 6 member community more stable than it would be without such predation. Thus raptors both stabilize and destabilize these communities. Models investigated by others (e.g. Yodzis 1977, Caswell 1978) also show that predation on competitors can increase or decrease community stability, as has been found in real communities (e.g. Paine 1966, Janzen 1976).

Fluctuations on prey populations mediate coexistence of competitors in nonequilibrium communities (Levins 1979). However, prey fluctuations may cause the loss of 1 *Mustela* species from the community when prey populations are low. Thus, a characteristic of the community that leads to coexistence of 2 *Mustela* at one time leads to the loss of 1 at other times.

Stability of *Mustela* communities over long periods may never be possible even though several factors mediate competition between *Mustela* species. Fluctuations in *Mustela* population sizes are common and several studies show that species become locally extinct for various periods of time (e.g. Lockie 1966, Fitzgerald 1977). This agrees with our computer simulation in which both *Mustela* species almost became extinct at different times and then recovered. We believe these fluctuations are the final explanation for coexistence of 2 or more *Mustela* species — coexistence is temporary. Two or more *Mustela* species may coexist when prey populations are high, especially if predation reduces competition and prey populations fluctuate. When prey populations decrease we expect that only 1 *Mustela* species will remain and that initial population sizes, reproductive adaptations, and predation abilities on different prey will determine which species remains, which goes extinct locally, and when recolonization by the eliminated species occurs.

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