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ECOLOGICAL IMPLICATIONS OF RESOURCE DEPRESSION

ERIC L. CHARNOV,* GORDON H. ORIAN,† AND KIM HYATT‡

A common but not universal consequence of the foraging activities of a predator is a lowering of capture rates with prey in its immediate vicinity. This may result from a number of different processes and need not require actual harvesting of any prey items by the predator. We term this phenomenon "depression" and its ecological consequences are the focus of this paper.

A great deal of attention has been devoted to implications of changes in prey *abundances* as a result of the activity of predators. We will focus on changes in prey *availability* strictly in terms of the perspective of actual or potential predators. Potential here refers to predators who may visit the site shortly after "the prey have been depressed." Depression phenomena are familiar to most field ecologists but are seldom incorporated into formal ecological theory.

While they are not really separate, it will be useful to divide our discussion into several sections, each focusing on a different question. (1) What are the processes by which prey might be depressed? (2) What are the characteristics of prey which affect their depressibility? Their recovery from the depression? (3) Are there prey that cannot be depressed? (4) What are the implications of depression from the viewpoint of a single predator individual? (5) Since prey depressed for one kind of predator are not necessarily depressed for another kind, what are the implications for competition theory? Here we are concerned with the possibility of *enhancement* of availability, as well as competition.

PROCESSES BY WHICH PREY ARE DEPRESSED

When capture rates are lowered because prey items are actually harvested by the predator, we term the effect "exploitation depression." Because no environment is really homogenous, it is expected that the more susceptible prey individuals are taken first. F. E. Smith (1972) has termed this "losing your marbles" after the following simple game. If a "predator" hunts for marbles on a grass lawn and returns to the grass those "captured" by tossing them over

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its shoulder, the capture rate will fall as the game progresses. While density of marbles remains constant, the "predator" selects for marbles that get lost in the grass.

It is not necessary, however, that prey be harvested for their availability to be depressed. As a result of the passage of predator A through an area, the prey may change their behavior in ways that make themselves more difficult to capture by A or a second predator B. This may involve changes in flocking behavior, greater alertness, or reduction of activities that increase risk to predation—for example, advertising, courting, and feeding. Depression caused in this manner we term "behavioral depression" and its magnitude may be independent of capture of any prey by the predator. Closely allied to this is what might be termed "microhabitat depression." A common response of prey to predators is to change position. These movements should evolve to place the prey in a location where the predator causing the disturbance finds it harder to encounter or capture the prey than in the original position. These two are often not distinct in that a shift in position is usually accompanied by a change in behavior. However, under some circumstances the implications for predator behavior are different under the two. If the depression is mostly a change in position, the prey may be still or more available to a second predator using a different method of hunting. If the change is increased alertness, it is likely that any predator hunting in the same spot soon after would suffer reduced capture rates. The microhabitat shift differs from exploitation in that the latter probably does not make prey available in other places, it simply removes prey from particular places. Recovery from exploitation is normally on a much larger time scale than from microhabitat shift.

A change in prey microhabitat and behavior (making them more difficult to capture) due to the presence of a predator is nicely illustrated in the following experiment. We used mayflies (Baetidae sp. unknown) as prey and Kokanee Salmon (*Oncorhynchus nerka*) as a predator with an experimental universe consisting of a 50-gal aquarium with a dark slate bottom. Since the edges were dark metal, the four corners were dark and earlier experiments demonstrated that the risk of attack was lower for a mayfly in a corner. Figure 1 shows the differences in the distribution of mayflies in the tank with or without a predator. Even though the predator was satiated and was not actively hunting (although it would sometimes chase a prey item) the mayflies moved to the corners when a fish was in the tank. In similar experiments with a substrate of gravel, leaves, sticks, etc., the movement was down or under, rather than to a corner, but the effect on availability to the predator was the same. Goss-Gustard (1970) has also demonstrated this effect for a wading bird, the Redshank (*Tringa totanus*) walking over a mud flat.

SOME CHARACTERISTICS OF PREY IMPORTANT IN DEPRESSION

It is useful to think of a site as recovering from depression, that is the availability of prey (to a predator of the type causing depression) going back up. In the case of exploitation, the recovery of capture rates with time following depression depends on birth and growth rates of individuals already on the site

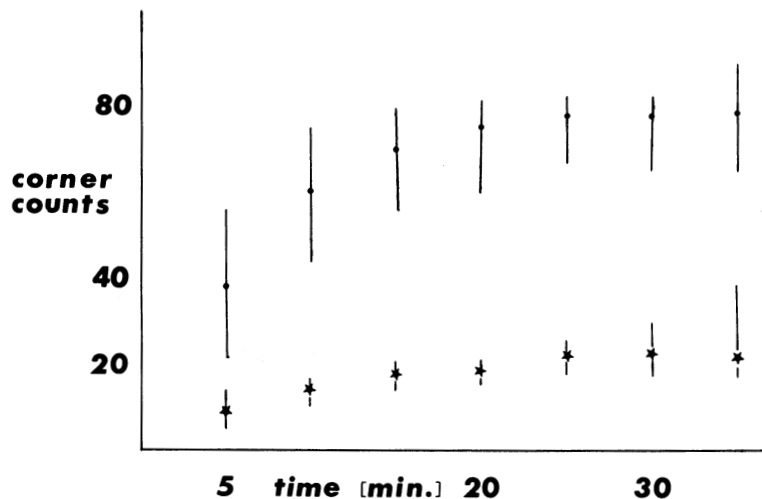


FIG. 1.—Depression of prey availability by a fish. One hundred mayfly nymphs were placed in a 60-gal aquarium. The corners of the tank were dark and provided a refuge from predation. In the absence of the predator about 20% of the prey were in the corner. In the presence of a predator (*Kokanee*, *Oncorhynchus nerka*) about 80% were hidden. Dot indicates predator present; star indicates predator absent; vertical bars indicate the range of 5 replicates.

and immigration of individuals from other areas. Other areas may be external to the site or may be other microhabitats at the site.

Recovery from microhabitat or behavioral depression can potentially be very rapid because the prey individuals need only return to their original positions or behavior, which may require but a few seconds. Nevertheless it may not be advantageous for them to do so and the depression effect may persist for a longer period of time. The rate of return to the original position is influenced primarily by (a) the risk to the prey from remaining in the new location, (b) the significance of the loss in energy intake (if the activity interrupted is feeding) caused by remaining in the new location which is, presumably, a poorer one for feeding, (c) the risk during the movement from the new to old location, (d) the risk if back in the original position, and (e) the loss per unit time incurred by failure to attend to activities (advertising, courting, mating) that may have been interrupted. The risk of remaining in the new position depends on the abundance of predators adapted to locate prey in that type of microhabitat (e.g., predators within the benthos that eat mayflies); that is, it is directly related to the probability that the next predator to visit the general location is one adapted to find prey in the new microhabitat.

The significance of the loss in feeding time may depend on the general availability of food and, hence, the need to search continuously, and the foraging mode of the prey. For example, small herbivores, many of which are highly vulnerable to predators when they are foraging, can be categorized as continuous or discontinuous feeders. Continuous feeders, of which most lepidopteran larvae and some microtine rodents are good examples, are adapted for rapid and continuous processing of leaf materials and need to feed most of

the time to achieve maximum growth and reproductive rates. Interruption of feeding thus increases developmental time and, consequently, the probability of being taken by a predator before reaching adulthood. For these species the consequences of interrupting feeding are more serious.

Intermittent feeders, on the other hand, normally feed for short bouts and then spend the bulk of their time processing the food in relatively safe sites. For such prey, extensive interruption of feeding may have little or no effect on developmental or reproductive rates and recovery may well be much longer for these prey than for continuous feeders.

Some other examples may be drawn from studies on birds. During the winter in the temperate zone, small birds must forage most of the daylight hours to gain enough energy (Gibb 1958, 1960) and most of them go to roost at night with reserves so small that they cannot last more than one night and part of the following day before they begin to starve (King 1972). Under these circumstances the penalty of not returning quickly to foraging may be severe and behavioral depression should be short-lived. In contrast, during periods of food excess, alertness toward predators could be maintained for a long time with little penalty. Similarly, during a time of establishment of territories, interruption of advertising for even a short period of time might result in occupancy of the area by a challenger whose eviction may require even more investment in activities riskier than simple advertising. Therefore, rapid resumption of advertising might be expected at this time during the annual cycle and the depression effect will rapidly disappear. These examples are merely suggestive of some of the factors that should be important in the recovery of a site from depression. Recovery is important since it determines when a site can be profitably revisited by a predator of the same type or whether or not the next predator(s) visiting the site will do better using other methods of hunting.

An interesting question is whether there are types of prey that cannot be depressed or that recover so rapidly that subsequent encounter rates are insensitive to previous harvesting. One example is perhaps photons of light that are "preyed" upon by photosynthetic plants. Though photons are "consumed" and, hence, instantaneously depressed by the plants, they are also instantaneously replaced so that the encounter rates of leaves with photons are independent of the rate of exploitation. Similarly, encounter rates of many sessile marine filter-feeding animals with their planktonic prey are probably unaffected by the harvesting rates of the predators, even if a volume of water is completely filtered, since the source area of the prey is huge and the prey are effectively renewed with each wave. Not surprisingly, for both these groups, the effective nondepressibility of the prey results in an intense competition for space, the necessary resource for access to the instantly renewed prey supply, and often favors a sessile strategy. Nevertheless, availability of prey is not uniform—that is, there are shadier spots, and waves in different regions carry different densities of plankton—so that sites may be ranked according to average intake rates.

The supply of emerging aquatic insects exploited by several species of breeding blackbirds in western North America also recovers quickly because the rate of emergence of new insects from the adjacent water is so rapid that the

encounter rates with prey are not determined by the rate of predation but primarily by the rate at which new prey are emerging from the water (Willson 1966; Orians 1966; Orians and Horn 1969). The movement of insects into spider webs and the drift of prey to the nets and filters of stream-inhabiting insects probably also occur at rates largely independent of the harvesting of the prey by predators. Similarly, the availability of cyclical cicadas to above-ground predators is presumably insensitive to predation on the adults. All these examples share the features that the prey are highly mobile and are drawn from a large pool that, for various reasons, cannot be directly tapped by the predators causing the instantaneous depression. Lacking such an external pool, however, recovery is a composite of birth, growth, and a much lower immigration rate, together with microhabitat shifts of prey already within the foraging area. Consequently, recovery rates are in general much longer.

DEPRESSION AND THE CHARACTERISTICS OF INDIVIDUAL PREDATORS

The postulate of decreasing capture rates at a site for a certain predator raises some interesting points relative to predator behavior. We first discuss the case of a lone predator in an environment where it is the sole cause of the depression. Suppose that we have an infinite environment made up of two patch types and a predator that hunts within patches but spends time in traveling between them. During a particular foraging bout, let the patches have a density such that t is the average travel time between patches and let P_A or P_B be the proportion that are of type A or B . While in a particular patch, the predator reduces the food availability such that the within-patch capture rate is a decreasing function of the time spent in the patch. The total amount of food taken from a patch ($f[T]$) thus rises from zero at a negatively accelerated rate (with time spent in the patch, T) to an asymptote represented by the total amount of food present in the patch to begin with. Let T_A denote the time spent in a patch of type A (T_B for B). The average time to use one patch (\bar{T}) is the travel time plus the time spent in the patch:

$$\bar{T} = t + P_A \cdot T_A + P_B \cdot T_B. \tag{1}$$

The average amount of food taken from one patch (\bar{E}) is

$$\bar{E} = P_A \cdot f_A(T_A) + P_B \cdot f_B(T_B). \tag{2}$$

\bar{E}/\bar{T} is an average rate of food intake, and the predator wishes to maximize it in the choice of T_A and T_B . This assumption of energy intake rate maximization is reasonable if there is no predation risk to the forager and if the movements are solely to gain energy. An example where it might not hold is where search for food and mates goes on simultaneously, as in some insects. To do this maximization, we set

$$\partial[\bar{E}/\bar{T}]/\partial T_{A \text{ or } B} = 0. \tag{3}$$

This gives a rule that $\partial[\bar{E}/\bar{T}]/\partial T_i = 0$ when

$$\frac{\partial f_i(T_i)}{\partial T_i} = \bar{E}/\bar{T}, \tag{4}$$

the same for all patch types in the habitat. Equation (4) states that the predator should leave a patch when the rate of food intake in that patch drops to the average for the habitat. Thus the predator need only know "how well it is doing" on the average and in its immediate neighborhood to make the decision to leave (or stay in) the present patch. This decision process is over a short time interval (i.e., within a single foraging bout) since implicit in the formulation is the assumption that the predator does not revisit patches. This result is further developed by Charnov (1973, 1975). A similar result is in Emlen (1973).

Laboratory experiments to test (4) were carried out with chickadees by Krebs, Ryan, and Charnov (1974). They defined the time between the last capture and when an individual left a patch (several wood blocks with holes for mealworms, suspended from an artificial tree) to go to another patch as the "giving up time" (GUT). This was taken to be a measure of the inverse of the capture rate when the bird left the patch. The experimental design consisted of two environments. In the first the average rate of food intake was high, in the second it was low. Within each environment there were two or three patch types, with each type having a specified number of mealworms. Statistical tests showed the GUT to be constant across patch types within an environment but to be lower on the average in the rich environment. This supports the two major predictions of the model.

Smith (1974*a*, 1974*b*), in some field experiments with thrushes, found that the tendency of a bird to remain in the area where it had already made a capture was greater the lower the overall availability of food in the habitat.

There are little other data that will allow more critical tests of the model although there are many data relating to gross predator behavior relative to clumps of prey. The simple tendency for a predator to remain in the area where it was successful has been documented for birds (Tinbergen et al. 1967; Krebs et al. 1972); fish (Beukema 1968); insects (Hafez 1961; Fleschner 1950; Laing 1938; Mitchell 1963; Dixon 1959, 1970; Banks 1957; Richerson and Borden 1972; Hassell and May 1973; Murdie and Hassell 1973). Even unicellular predators exhibit increased frequency of turning following an encounter with food particles, a behavior pattern which results in a more intensive search of the vicinity of the capture (Fraenkel and Gunn 1940; MacNab and Koshland 1972).

Whether or not a predator has exclusive use of an area relative to similar predators, it may gain by employing several different methods of hunting in the same patch. If the depression is a microhabitat shift, a new searching method might increase the capture rate in a previously covered patch. The predator might well employ a definite sequence of hunting methods in the course of a foraging bout but we know of no relevant data.

COEXISTENCE OF PREDATORS

A predator with one hunting mode may cause a microhabitat shift of a particular kind of prey so as to make it more available to a predator with a different hunting mode. For prey depressed purely in a behavioral way (e.g.,

TABLE 1
DIETS OF LARGE VERTEBRATE PREDATORS IN THE FOOTHILLS OF THE
SIERRA NEVADA, CALIFORNIA

PREY	PREDATOR			
	Horned Owl	Coyote	Red-tailed Hawk	Rattlesnake
Cottontail	61.1	45.5	24.2	15.2
Woodrat	17.9	4.9	1.1	1.7
Kangaroo Rat	4.5	3.3	0.2	5.9
Pocket Gopher.....	4.3	3.5	7.4	2.4
Gopher Snake.....	3.7	6.0	9.0	0.0
Ground Squirrel.....	2.4	31.2	49.5	70.5
Others	6.1	5.7	8.6	4.2

SOURCE.—From Fitch (1947).

NOTE.—Data are expressed as % composition by volume.

increased alertness, etc.) we should expect less enhancement, because their alertness may make them less available for most other predators. The increased awareness shown by ungulates in the presence of a hunting lion probably also decreases their vulnerability to other potential predators, especially those that hunt by stealth. On the other hand, a ground squirrel watching the sky for a hawk may be more susceptible to an attack by a weasel.

While we will stress here enhancement of availability as a result of depression, this of course need not be so. Where behavioral or microhabitat depression is important predators may divide up the resource by (1) simply hunting in a different way, (2) hunting at a different time (getting to a patch first?), and (3) hunting in a different place. Only alternative (3) has played a major role in competition theory although Schoener (1974) notes that predators of active prey are more likely than other groups to hunt at different times of the day. A great deal of theory exists on competition in terms of diet overlaps (MacArthur 1972; Cody 1974; Schoener 1974). We are more concerned at this juncture with the possibilities of enhancement of encounter rates with prey resulting from the activities of other predators. There is considerable indirect evidence that such enhancement may be important in the structure of ecological communities.

It has been known for some time that clusters of predators of different morphologies and behavior may show very high overlaps in diet, higher than can be found among coexisting predators of closer taxonomic affinities. For example, in the foothills of the Sierra Nevada in California coexisting populations of Red-tailed Hawks (*Buteo jamaicensis*), Horned Owls (*Bubo virginianus*), Coyotes (*Canis latrans*), Bobcats (*Lynx rufus*), and Rattlesnakes (*Crotalis viridis*) overlap extensively in prey taken (table 1). Using these data to estimate competition coefficients, despite our prior warnings, we obtain the alpha values shown in table 2 which are much higher than normally characteristic of congeneric or confamilial coexisting species. This pattern is typical of Red-tailed Hawk and Horned Owl populations in other parts of their range (Orians and Kuhlman 1956). We suspect that this coexistence is possible because of the impossibility of behavioral exclusion among members of these assemblages of

TABLE 2
OVERLAPS IN DIETS OF LARGE VERTEBRATE PREDATORS IN THE
FOOTHILLS OF THE SIERRA NEVADA, CALIFORNIA

	Horned Owl	Coyote	Red-tailed Hawk	Rattlesnake
Horned Owl	1	.84	.65	.44
Coyote	1	.93	.85
Red-tailed Hawk.....	1	.89
Rattlesnake	1

NOTE.—Data calculated using Horn's (1966) index of overlap. Overlap is assumed to be complete in the "others" category.

predators together with the probability that their activities are enhancing or, at the least, that the enhancement significantly reduces the amount of depression caused. For example, mammalian predators hunting beneath bushes and in dense cover may cause a movement of prey into more open areas where vulnerability to avian predators is increased. Risks from owl predation at night may cause prey to begin to forage earlier in the evening and to continue later into the morning than would otherwise be the case, thereby increasing availability to hawks, etc.

Another well-known example of enhancement is the association of aquatic birds with schools of predatory fish. The activities of predatory fish, such as tuna or tarpon, result in a movement of prey fish to the surface, often with actual breaching. Thus the prey which are unavailable to birds if they remain lower in the water, can be captured when they are attempting to escape from larger fish (Zaret and Paine 1973). In this case it is likely that predation from fish is more important than predation by birds at the surface, so that the smaller fish in their behavior can be expected to be "predator foolhardy" in relation to the birds, further enhancing their availability.

If the activities of one predator actually enhance encounters with prey for another predator, it may be advantageous for the second predator to forage near the first. The ideal individual to follow would be one that disturbed a large number of prey but pursued and/or captured few of them. If this process is actually a significant factor favoring foraging in groups, a number of relationships ought to hold true. First, individuals of some species should be followed much more often than they themselves elect to follow individuals of other species. Second, since individuals that disturb many prey but take only a few are likely to enhance encounters for both individuals of other species as well as for conspecifics, they should tend to form intraspecific foraging flocks as well as being regularly joined by individuals of other species. Third, agonistic encounters should be common among individuals in mixed foraging flocks because their foraging activities should regularly bring them into direct competition for individual prey items. Fourth, individuals that forage in ways that are unlikely to enhance prey encounter and capture possibilities for other individuals should not be joined by those individuals.

These predictions can be tested with the extensive data gathered by Moynihan (1962) on mixed species foraging flocks of birds in Panamá. Moynihan found characteristic association patterns among species, some species being regularly joined and followed while others are joiners but are seldom joined. In the lowland mixed tanager-honey creeper flocks, the species most often joined by individuals of other species was the Plain-colored Tanager (*Tangara inornata*). Foraging individuals of this species frequently engage in exaggerated wing-flicking and tail-flicking movements and are constantly active and changing perches. Nonetheless, they do not regularly pursue flushed prey. These behavior patterns are also typical of the Brown-capped Bush-tanager (*Chlorospingus ophthalmicus*), the species most commonly followed in the montane mixed flocks. These foraging behaviors, which apparently function to cause startle responses among the prey, are exactly those expected to produce a strong enhancement effect for other nearby individuals (prediction 1). Both of these species are also highly gregarious intraspecifically (prediction 2).

These two nuclear species are joined by a variety of generalized foragers which may benefit from the enhancement, but they do not apparently benefit the nuclear species which are regularly observed to engage in agonistic behavior toward followers (prediction 3). The members of the mixed tanager and honey-creeper flocks, so characteristic of lowland Panamá, are restricted to a rather narrow vertical layer of vegetation and frequently feed on similar foods. Most of the species are generalists that exploit a variety of fruits and arthropod prey and they regularly engage in supplanting attacks with other flock members.

Similar observations were obtained on mixed feeding flocks in Borneo and Papua New Guinea (D. L. Pearson, personal communication). For example, Fan-tailed Flycatchers (*Rhipidura perlata* in Borneo; *R. rufiventris* in Papua New Guinea) forage with constant wing and tail flicking and both are followed extensively by many other species. *Rhipidura rufiventris* is often joined by a smaller congener, *R. rufidorsa*, which does not use wing and tail flicking consistently. On several occasions *R. rufidorsa* was observed hunting close to a foraging *R. rufiventris*, sallying out after insects disturbed by the latter. The Rufous Babbler (*Pomatostomus iridorei*) on New Guinea forms the nucleus of many large mixed species foraging flocks and is always found in intraspecific flocks. It forages in dead leaves and tangles and regularly causes insects to fly out. It never pursues these insects, however, but many smaller species forage close to the babblers and profit from their foraging activities.

The Slate-throated Redstart (*Myioborus miniatus*) and the Collared Redstart (*M. torquatus*), both common in the montane regions in Panamá, also forage actively and in such a manner as to disturb many prey, but unlike the tanagers they regularly pursue the prey they disturb and capture a large fraction of their prey on the wing. Both are rather solitary foragers and sometimes join in mixed feeding flocks but do not do so regularly and they do not form intraspecific flocks. Slate-throated Redstarts are joined by individuals of other species very infrequently, Collared Redstarts more so. The previous hypothesis predicts their low enhancement value but does not explain the differences

between them. Collared Redstarts replace Slate-throated Redstarts at higher elevations where perhaps differences in foraging conditions or prey types might change the enhancement pattern.

Another pattern noted by Moynihan (1962) is that the Central American species most often joined and followed by others tend to have narrow geographical ranges while those that are the most active followers have broad ranges. One possible interpretation is that the species being followed are more specialized in their foraging, and hence have narrow ranges compared to the more generalized followers. A specialized forager, provided it disturbed large numbers of prey, would be worth following more than a generalist that was likely to pursue and capture a larger proportion of the prey it affected.

The above analysis suggests that enhancement is a likely candidate to explain several features of the flocking behavior of insectivorous or partially insectivorous birds. It is obvious, however, that enhancement cannot explain flocking of seed- and fruit-eating birds. Moreover, demonstrating a probable role of enhancement among insectivorous species does not exclude the possibility that protection from predation may be involved as well. In addition to the greater general level of awareness of predators of grouped individuals there may be a particular advantage to associating with individuals of other species that have different escape behavior patterns. This would make it more difficult for a predator to predict the escape behavior of any individual it elected to pursue than would be the case if all the individuals were of the same species. Intraspecific escape behavior polymorphism might be expected to evolve in these cases as well (Fisher 1958).

Another well-documented case of enhancement effects of one predator allowing the existence of other species in an area is the association of birds with neotropical army ant swarms (Willis 1966, 1969). The obligate ant-following species probably could not exist without the prey-flushing activities of the ants and populations of the facultative followers may be denser than they would otherwise be.

EVOLUTION OF TERRITORIALITY

This section will treat territoriality in light of the concept of depression. We are aware of the large literature on the subject (cf. Brown and Orians 1970; Stokes 1974) and only mean to suggest that depression could play a role.

The time between initial depression and when a predator can profitably revisit a given patch is called the return time. If the patch is subject to visitation by other predators causing the same kind of depression, this return time may be very difficult for the predator to estimate. An important consequence of holding exclusive space (territoriality) may be the improvement of estimates of the return time for various patches. This would allow the owner to revisit in such a manner to increase its food intake. That territories are defended against conspecifics or very similar species is consistent with this notion as these are the individuals most likely to cause the same kind of depression. However, the nature of intraspecies competition is different since reproductive competition

for mates is also potentially present. Thus the potential loss in fitness for a given level of depression is greater with a conspecific competitor. This also suggests that territory size may be related to the depression-revisit-depression cycle for the various patches that make up the territory. Further it suggests that species which show respect for territorial boundaries in the absence of aggression (e.g., respect for scent information in some Canids or Felids) or show more or less exclusive use of areas may do so because the "owner" has information about depressed and nondepressed patches which is lacking to the potential intruder. The potential intruder can use the information about boundaries to avoid the unknown areas. This requires that the potential intruder gain by the avoidance decision, which is the case if it possesses its own area. Individuals without a territory or those whose territory has declined in value may find it advantageous to invade the areas of others. We might expect overt aggression on the part of the owner toward these migrant individuals which would force them into the position of moving from territory to territory, without staying very long in any one place.

CONCLUSIONS

We have attempted to show that resource depression is an important component of predation which may be independent of the actual amount of exploitation of the prey. In featured environments, where behavioral and microhabitat changes in the prey are important, depression due to these factors may be more important than exploitation depression. If so, then the straightforward measurement of overlap of diets of predators, the usual information used to estimate competition coefficients for theoretical analysis, may be very misleading. This emphasizes the importance of knowing the ecological and behavioral attributes of the organisms under study as thoroughly as possible.

The susceptibility of the prey to depression and the relative importance of exploitation, behavioral and microhabitat depression, should be incorporated into analysis of the significance of differences in foraging mode and time of foraging on potential competition. For example, seeds constitute a resource readily depressed by exploitation but without behavioral or microhabitat shifts. For such a resource the time of day of exploitation would presumably be of no competitive significance, but the mode of searching might be. A bird capable of gapping, probing, or scratching should find seeds not available to a surface gleaner. On the other hand, herbivorous insects exhibit strong behavioral and microhabitat shifts, and slight differences in the timing of exploitation and order of appearance of predators might be important in the kinds and number of prey found. Also, for predators on these prey types, divergence in searching mode and microhabitat selection may be more critical in reducing competition than the taxonomic overlap in prey taken. Such considerations need to be programmed into conceptual analyses of predation and competition more than they have heretofore.

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LITERATURE CITED

- Banks, C. J. 1957. The behavior of individual coccinellid larvae on plants. *J. Anim. Behav.* 5:12-24.
- Beukema, J. J. 1968. Predation by the three-spined stickleback (*Gasterosteus aculeatus*): the influence of hunger and experience. *Behavior* 31:1-126.
- Brown, J. L., and G. H. Orians. 1970. Spacing patterns in mobile animals. *Ann. Rev. Ecol. and Syst.* 1:239-262.
- Charnov, E. L. 1973. Optimal foraging: some theoretical explorations. Ph.D. diss. University of Washington.
- . 1976. Optimal foraging: the marginal value theorem. *Theor. Pop. Biol.* (in press).
- Cody, M. L. 1974. Competition and the structure of bird communities. *Monogr. Pop. Biol.* Princeton University Press, Princeton, N.J. 318 pp.
- Dixon, A. F. G. 1959. An experimental study of the searching behavior of the predatory coccinellid beetle *Adalia decempunctata*. *J. Anim. Ecol.* 28:259-281.
- . 1970. Factors limiting the effectiveness of the coccinellid beetle, *Adalia bipunctata*, as a predator of the sycamore aphid, *Depanosiphum platanoides*. *J. Anim. Ecol.* 39:739-751.
- Emlen, J. M. 1973. *Ecology, an evolutionary approach*. Addison-Wesley, Reading, Mass. 493 pp.
- Fitch, H. S. 1947. Predation by owls in the Sierran foothills of California. *Condor* 49:137-151.
- Fisher, R. A. 1958. Polymorphism and natural selection. *J. Ecol.* 46:289-293.
- Fleschner, C. A. 1950. Studies on search capacity of the larvae of three predators of the citrus red mite. *Hilgardia* 20:233-265.
- Fraenkel, G. S., and D. L. Gunn. 1940. *The orientation of animals*. Oxford University Press, London.
- Gibb, J. A. 1958. Predation by tits and squirrels on the eucosmid *Ernarmonia conicolana* (Heyl.) *J. Anim. Ecol.* 27:275-296.
- . 1960. Populations of tits and goldcrests and their food supply in pine plantations. *Ibis* 102:163-208.
- Goss-Custard, J. D. 1970. Feeding dispersion in some overwintering wading birds. *In* J. H. Crook, ed. *Social behavior in birds and mammals*. Academic Press, New York.
- Hafez, M. 1961. Seasonal fluctuations of population density of the cabbage aphid *Brevicoryne brassicae* (L.) in the Netherlands and the role of its parasite *Aphidius (Diaretiella) rapae* (Curtis). *Tijdschrift over Plantenziekten*. 67:445-548.
- Hassell, M. P., and R. M. May. 1973. Stability in insect host-parasite models. *J. Anim. Ecol.* 42:693-726.
- Horn, H. S. 1966. The measurement of "overlap" in ecological studies. *Amer. Natur.* 100:611-617.
- King, J. R. 1972. Adaptive periodic fat storage by birds. *Proc. XV Int. Ornith. Congr.* 200-217.

- Krebs, J. R., M. H., MacRoberts, and J. M. Cullen. 1972. Flocking and feeding in the Great Tit, *Parus major*—an experimental study. *Ibis* 114:507–530.
- Krebs, J. R., J. C., Ryan, and E. L. Charnov. 1974. Hunting by expectation or optimal foraging? a study of patch use by chickadees. *J. Anim. Behav.* 22:953–964.
- Laing, J. 1938. Host finding by insect parasites II: the chance of *Trichogramma evanescens* finding its hosts. *J. Exp. Biol.* 15:281–302.
- MacArthur, R. H. 1972. Geographic ecology. Harper & Row, New York.
- MacNab, R. M., and D. E. Koshland. 1972. The gradient-sensing mechanism in bacterial chemotaxis. *Proc. Nat. Acad. Sci.* 69:2509–2512.
- Mitchell, B. 1963. Ecology of two carabid beetles, *Bembidion lampros* and *Trechus quadristriatus*. *J. Anim. Ecol.* 32:289–299.
- Moynihan, M. 1962. The organization and probable evolution of some mixed species flocks of neotropical birds. *Smithsonian Misc. Collections* 143:1–140.
- Murdie, G., and M. P. Hassell. 1973. Food distribution, searching success and predator-prey models. In M. S. Bartlett, and R. W. Hiorns, eds. *The mathematical theory of the dynamics of biological populations*. Academic, London.
- Orians, G. H. 1966. Food of nestling yellow-headed blackbirds in Cariboo Parklands, B.C. *Condor* 68:231–237.
- Orians, G. H., and F. Kuhlman. 1956. Red-tailed Hawk and Horned Owl populations in Wisconsin. *Condor* 58:371–385.
- Orians, G. H., and H. S. Horn. 1969. Overlap in foods of four species of blackbirds in the potholes of Central Washington. *Ecology* 50:930–938.
- Richerson, J. V., and J. H. Borden. 1972. Host finding of *Coeloides brunneri* (Hymenoptera: Braconidae). *Can. Entomol.* 104:1235–1250.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- Smith, F. E. 1972. Spatial heterogeneity, stability and diversity in ecosystems. In E. S. Deevey, ed. *Growth by intussusception*. *Trans. Connecticut Acad. Arts and Sci.* 44:310–335.
- Smith, J. N. M. 1974a. The food searching behavior of two European thrushes I. Description and analyses of search paths. *Behavior* 48:276–302.
- . 1974b. The food searching behavior of two European thrushes II. The adaptiveness of the search patterns. *Behavior* 49:1–61.
- Stokes, A. W., ed. 1974). *Territory*. Dowden, Hutchinson & Ross, Stroudsburg, Penn. 398 pp.
- Tinbergen, N., M. Impekoven, and D. Franck. 1967. An experiment on spacing-out as a defense against predation. *Behavior* 38:307–321.
- Willis, E. O. 1966. Competitive exclusion and the foraging behavior of plain-brown woodcreepers. *Ecology* 47:667–672.
- . 1969. On the behavior of five species of *Rhegmatorhina*, ant-following antbirds of the Amazon basin. *Wilson Bull.* 81:363–395.
- Willson, M. F. 1966. The breeding ecology of yellow-headed blackbirds. *Ecol. Monogr.* 36:51–77.
- Zaret, T. M., and R. T. Paine. 1973. Species introduction in a tropical lake. *Science* 182:449–455.