

# Territory size and location in animals with refuges: influence of predation risk

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## Summary

Territory size is usually explained by balancing the benefits of increased size against the costs of defense. An alternative hypothesis for animals that maintain refuges is that the costs of large territories lie in the predation risk associated with leaving the refuge. An optimum territory size is discovered, given only this cost and no cost of defense. Predation risk is also considered a determinant of the value of a territory's location within a colony. Risk relative to location is discovered to be a binary variable, either low or high, depending upon the speed of the predator.

*Keywords:* Territoriality; refuges; predation; coloniality.

## Introduction

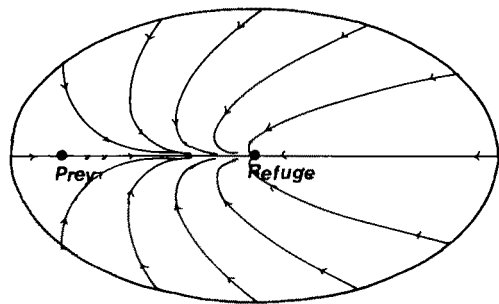
Predation risk is not often considered to be a factor contributing to territoriality, other perhaps than in establishing the value of secure habitat types within a territory. The only published empirical data on the effect of predation on territory holders suggest that it may interfere with the maintenance of areas of exclusive use. Myers (1984) discovered that the presence of a Merlin (*Falco columbarius*) caused Sanderlings (*Calidris alba*) to abandon profitable territories. The cost of not flocking in this high-risk situation apparently exceeded the benefit of defending resources.

Covich (1976) has pointed out that in sedentary species with refuges, departure from the refuge is dangerous. The risk of capture when distant from the refuge might impose a limit on the size of such an animal's home range. A territory, by definition, is that portion of the home range defended against other potential users; as a consequence, an argument accounting for home-range size does not necessarily explain the size of a territory. Yet it seems a small evolutionary step for an animal with a constrained home range centered on a refuge to begin actively defending that area. Here I formalize Covich's argument with specific reference to territoriality in ground squirrels and other ground-living rodents.

## A model of territory size

The only existing theoretical treatment of refuge use in the face of pursuit by a predator is a neglected paper by Lotka (1932). Lotka developed a deterministic model of a dog pursuing a rabbit toward a refuge. Figure 1 displays his main result: the area around the refuge divides into two zones, an area in which capture is certain and an area in which escape is certain. The boundary between these regions is an ellipse centered on the refuge. The prey is at one focus, and the eccentricity of the ellipse is the ratio of the top speeds of the prey and predator. Capture is certain if the predator is within the ellipse; escape is certain if it is outside. Lotka made a variety

Figure 1. Elliptical isochrone centered on the refuge. The prey is at one focus. A predator within the ellipse will capture with certainty. The lines are curves of pursuit predicted by the theory of Lotka (1932).



of simplifying assumptions to arrive at this result. I will not discuss these here, other than to note that several have been born out by subsequent research and none has been rejected. I shall take as a working hypothesis that the zone of potential danger around a refuge is a sharply bounded ellipse.

The basic argument requires two assumptions: in homogeneous habitats territories should be centered on the burrow, and departure from the burrow entails benefits in terms of resources to be gained and risks in terms of an increasing likelihood of being caught before returning. Others have pointed out the benefits of circular territories (reviewed in Covich, 1976), and it seems obvious here that around a single burrow a circular territory would maximize area while minimizing the average distance from the refuge. The fitness of an individual territory holder can, as a consequence, be expressed as  $W(r) = B(r) - C(r)$ , in which  $r$  is the radius of the territory,  $B(r)$  is the benefit or fitness gained from the resources obtained in a territory of radius  $r$  and  $C(r)$  is the cost or fitness lost by maintaining a territory of that size. The goal is to discover how fitness varies with  $r$ , and this requires the specification of reasonable forms for the functions  $B$  and  $C$ . Since the marginal value of the resources derived from an additional increment in the size of the territory should diminish as the total area increases, I assume a saturating, downwardly concave curve for  $B(r)$  as a function of area ( $A$ ). The precise algebraic form is not important, but the simplest is the Holling disc equation:

$$B(r) = \frac{aA}{1 + ahA} = \frac{a \pi r^2}{1 + ah \pi r^2} \quad (1)$$

where  $h$  is the resource processing time per unit area and  $a$  is the exploitation rate. This equation assumes that the territory is spatially homogeneous with respect to resource production and that the owner exploits it uniformly.

The fitness decrement,  $C(r)$ , is assumed to be proportional to the area of the elliptical zone of danger, centered on the burrow, with foci a distance  $r$  from the burrow and eccentricity ( $e$ ) equal to the ratio of the top speeds of the prey and the predator. The area of this zone of danger is  $\pi r^2 u$ , where  $u = \sqrt{(1 - e^2)}/e^2$ , and the fitness cost is some constant,  $\delta$ , times the area of the danger zone. These two curves,  $B$  and  $C$ , are shown in Fig. 2 as functions of  $r$ . Territoriality should not be expected when its benefits fail to exceed its costs. For this model, costs exceed benefits when  $\delta u > a$  or when  $r > \sqrt{(a - \delta u)/ah\pi}$ . Within the range of values of  $r$  where  $B - C > 0$ , fitness is maximum at:

$$r^* = \left[ \frac{(a/\delta u)^{\frac{1}{2}} - 1}{ah\pi} \right]^{\frac{1}{2}} \quad (2)$$

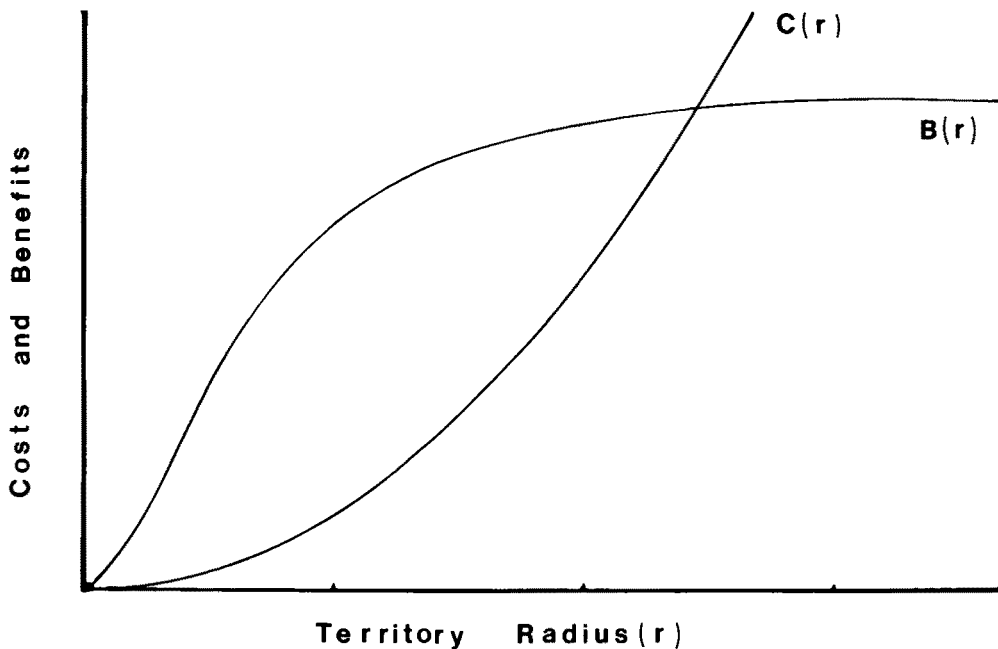


Figure 2. The benefits,  $B(r)$ , and costs,  $C(r)$ , of territoriality as a function of territory radius,  $r$ . Benefits are computed from Equation 1 with  $a = 1$ . Costs are proportional to the area of an ellipse with eccentricity  $e = 0.9$ .

Equation 2 makes intuitive sense from several perspectives: (1) Optimum territory size declines as both territory richness and resource processing time increase (Equation 1 reaches a plateau more quickly for higher values of  $a$  and  $h$ ). (2) Optimum territory size declines as the danger per unit area increases. (3) Since  $u$  increases with the predator's speed, the optimum territory is smaller when facing faster predators. Alternatively, for a particular predator, faster prey should have larger territories. I conclude that vulnerability to predators can generate the same qualitative fitness costs of increased territory size as aggressive defense.

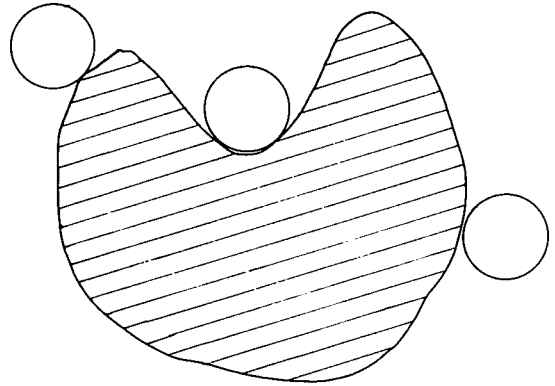
For many colonial animals the primary determinant of security is position within the colony. Next I develop arguments for colony shape and for how risk varies with position within a colony.

### Colony shape

The border of a colony is undoubtedly the most dangerous portion in which to live. Although a slow predator will not penetrate a colony far before eliciting alarm calls, it may easily ambush an animal on the margin of the colony. If the margin is such a dangerous place, one would expect it to be chosen as a site for a new territory only if no more-central locations are available. An animal forced to the fringes of the colony has the option of leaving it entirely or establishing a new territory on its boundary. Where the existing boundaries of the colony coincide with the limits of acceptable habitat, either because of availability of food or proximity to dangerous ambush sites, then the reasonable choice might be to leave. In a uniformly suitable habitat, I assume that a subordinate animal's best alternative is to settle on the periphery of the colony.

One can speculate on the factors an animal might consider when choosing a location on the border of the colony. I consider only the relative risk of predation associated with the new site.

Figure 3. A colony (shaded area) showing outwardly concave and convex regions of the border. The small circles represent possible sites for a new territory.



This will relate to a variety of features of the location, one of the most important being the amount of the new territory's periphery that is exposed to the outside of the colony. Were only proximity to the burrow important, the newly established territory would be circular and centered on the burrow. But an owner concerned with minimizing the proportion of the boundary exposed to the outside of the colony may need to distort this shape somewhat. An operational criterion of a quality site, therefore, may be that requiring the least distortion from circularity. Examination of Fig. 3 suggests that these high-quality sites will be outwardly concave. The worst sites, by comparison, will be the most convex; in fact the choice of a convex site may result in a good deal of exposure regardless of how the territory is distorted. If colony growth occurs by the establishment of new territories in the more concave sites, then colonies should end up uniformly convex or approximately circular.

### Risk versus location

The fringing territories are the most vulnerable to attack, but it does not follow that within this fringe the more central the territory, the more secure it is. I justify this assertion with the following argument. Impose a coordinate system on a circular colony such that its origin lies at the center of the colony and the x-axis lies along a line connecting the origin to any particular colony member, as in Fig. 4. Define the angle of approach of a predator as  $\gamma$ . If  $\gamma$  is uniformly distributed on the interval  $(0, 2\pi)$ , then the predator's direction of approach is unpredictable. If this predator is sighted by the colony at a distance  $d_p$  from the origin and if the potential prey (the

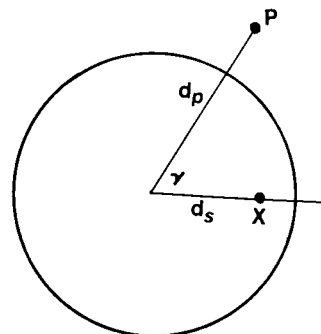


Figure 4. Geometry of the risk-versus-location argument. The colony member (X) is at a distance  $d_s$  from the center. The predator (P) is outside the colony's border at a distance  $d_p$  from the center. The line connecting it to the colony's center forms an angle  $\gamma$  with the line to the potential prey.

animal used to define the x-axis) is at a distance  $d_s$  from the origin, then the two animals will be separated by a distance  $s$ , where, from the Law of Cosines:

$$s = \sqrt{d_s^2 + d_p^2 - 2d_s d_p \cos \gamma} \quad (3)$$

Since the angle of approach is distributed uniformly over the circle, the mean distance from the predator is given by:

$$s = \frac{1}{\pi} \int_0^\pi (d_s^2 + d_p^2 - 2d_s d_p \cos \gamma)^{\frac{1}{2}} d\gamma = d_s^2 + d_p^2 \quad (4)$$

In other words the mean distance from the predator increases as the square of the distance from the center.

If mean distance were the important determinant of the risk of capture, then the safest locations would be on the fringes of the colony. This cannot be correct. Lotka concluded that risk does not vary continuously with distance from the predator but that there exists a threshold in security. Perhaps, then, the important variable in evaluating position within the colony is not the expected distance from an approaching predator but the probability that one will be within the critical danger zone of a predator approaching from a random direction. This is easily found.

Returning to Equation 3, I note that the minimum value of  $s$  is  $d_s - d_p$  (when  $\gamma = 0$ ) and the maximum value is  $d_s + d_p$  (when  $\gamma = \pi$ ). Between these two extremes, the distance from the predator increases monotonically with  $\gamma$ . The proportion of the range of values of  $\gamma$  in which  $s$  is greater than  $D$ , the danger threshold, is:

$$\Pr\{s > D\} = 1 - \frac{1}{\pi} \cos^{-1} \left[ \frac{d_s^2 + d_p^2 - D^2}{2d_s d_p} \right] \quad (5)$$

Figure 5 displays a graph of Equation 5, the probability that one is outside the zone of danger of a predator approaching from a random direction. Two qualitatively different patterns emerge from this figure. If the predator is sufficiently slow that the radius of the zone of danger surrounding the predator is less than the radius of the colony, then the centermost position is most secure. In this case, however, security does not diminish smoothly and gradually with distance from the center. There seem to be roughly two parts to the colony, a completely secure inner region and a less secure peripheral portion. Within each region vulnerability is approximately uniform. By comparison with this result, if the predator is sufficiently fast that its zone of danger overlaps the center of the colony, then the central region becomes the least secure portion of the colony.

The weakest of the assumptions underlying this unintuitive result is that animals within the critical distance of the predator are equally vulnerable to attack. Normally in arguments such as this, vulnerability is presumed highest in those prey closest to the predator (Hamilton, 1971; Vine, 1971). This seems to be the preferable assumption, at first glance, except that there is evidence in ground squirrels that it may not be true. Sherman (1985) observed a population of Belding's ground squirrels (*Spermophilus beldingi*) under attack by hawks. Those animals closest to the hawk were most likely to give alarm calls and least likely to be caught. Perhaps it would be worth considering whether, when the predator is much faster than the prey, an animal's proximity to the predator is a less significant determinant of its risk than its distance from the nearest burrow.

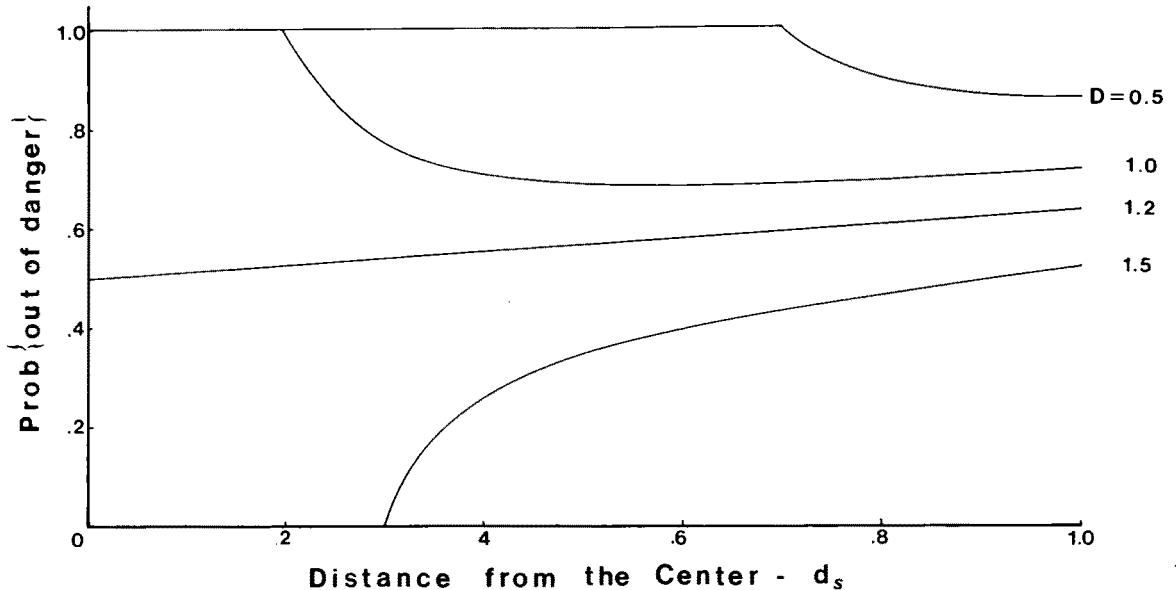


Figure 5. The probability that a colony member will be out of danger from a randomly approaching predator as a function of its distance from the colony's center. The radius of the colony is 1.0, and  $d_p$  is 1.2. The four curves represent different values of the critical distance,  $D$ .

## Discussion

Perhaps it is not surprising that an animal which relies upon a refuge to escape predation should find it necessary to restrict its activities to the vicinity of that refuge. However, that the risk of predation could as easily account for optimum territory size in such animals as defense against conspecifics seems to have escaped the attention of everyone but Covich (1976). I conclude that predation risk and aggressive defense provide alternative explanations of limits to territory size. The question arises as to how one is to discriminate between these costs of territoriality, given that the fitness components associated with either mechanism are difficult to measure and that the predicted optimum territory sizes may not differ.

There are a variety of ways to discriminate between these alternatives. Two strong tests are obvious. The first is to vary the costs of territorial defense. One could either compare the home ranges of two populations that differ in density (in areas of comparable productivity and predator activity) or compare territory size before and after an experimental reduction in colony size. The defense hypothesis predicts that the home ranges of animals in the less-dense population will be enlarged. The predation risk hypothesis predicts no change in territory size. A second test is to alter the nature of the predators which harass the colony. If, for example, one were to shift the predator complex from primarily mammalian to primarily avian, one would expect no change in the mean territory size under the defense model and a systematic decline under the risk model.

A tacit assumption of those who speculate about the benefits of aggregation to prey is that those at the fringes of a group are at the highest risk. Sherman's (1985) observations suggest that the nearest animal is not necessarily the most catchable, at least by hawks. Vulnerability in refuging animals may have a great deal more to do with proximity to a burrow than with proximity to the predator. If this is true, then the theory presented here suggests that the danger of an approaching slow predator in different portions of the colony is an approximately binary

variable. The low-risk area is a disc in the center of the colony, and the relatively high-risk area is a halo surrounding it. The relative sizes of the two subareas depend upon the actual speed of the slow predator. Small alterations of position within these areas make little difference in risk. I anticipate, therefore, that the opening of a territory in the center should be the cause for contest only among peripheral animals, and the opening of a territory in the more peripheral portion of the colony should occasion no contests at all. This result is reversed if the primary threat comes from fast predators, such as birds of prey. In this case the center is the most frequently attacked area, and the periphery is on average the safer place to live.

This argument notwithstanding, probably the worse place to locate is the actual colony boundary. There one is exposed to ambush attack from the entire community of predators. The slow predators that could not hope to penetrate the colony without being noticed will still be a danger to peripheral animals. These colony members should position themselves so as to maintain circular territories without exposing any more of their territory's boundary to the outside than necessary. This implies that they should choose locations as outwardly concave as possible, avoiding in particular very convex regions. The consequence of such choices is that in homogeneous environments colony growth will tend to a uniformly convex surface, approximating a circle.

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