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Interspecific Territoriality by a Rufous-Tailed Hummingbird (*Amazilia tzacatl*): Effects of Intruder Size and Resource Value[1]

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ABSTRACT

I studied two aspects of interspecific territoriality in a Costa Rican nectarivorous bird, the rufous-tailed hummingbird (*Amazilia tzacatl*). First, I examined variation in the response of the territory holder to four species of intruding hummingbirds by quantifying the proportion of intruders chased from the territory. This measure of territory defense varied significantly among species of intruders and was negatively related to the intruding species' body mass, possibly due to potential costs associated with becoming involved in escalated contests with larger individuals. Second, I tested for an effect of resource manipulation on territory defense. I increased the resource value of the territory by injecting extant natural flowers with artificial sucrose solution. While the frequency of territorial intrusions did not change, the proportion of intruders chased by the territory holder increased. Apparently, nectar supplementation changed the territory holder's perception of resource value but had little impact on the intruders' perception.

RESUMEN

Estudié dos aspectos de territorialidad interespecie en un colibrí nectarívoro de Costa Rica—el Amazilia Rabirrufa (*Amazilia tzacatl*). Lo primero, estudié la variación en la reacción del poseedor del territorio a cuatro especies de colibrís intrusos por cuantificando la proporción de intrusos que estaban echado fuera del territorio. Esta medida de defensa del territorio varió significativamente entre especies de intrusos, y estaba relacionada negativamente en el peso del intruso, posiblemente debiendo al costo potencial asociado con la posibilidad de competiciónes agravando con individuos más grande. Segundo, busqué un efecto en los niveles de defensa con la manipulación de recursos en un territorio. Aumenté los recursos en el territorio por inyecciónes de una sucrosa artificial en las flores naturales. La frecuencia de los intrusiones territoriales no cambió, pero la proporción de intrusos echaron fuera del territorio aumentó. Aparentemente, el néctar suplementario cambió la percepción del valor del territorio para el poseedor del territorio, pero no para los intrusos.

Key words: Amazilia tzacatl*; Costa Rica; hummingbird; La Selva; nectar; territoriality.*

TERRITORIALITY CAN BE DEFINED AS THE DEFENSE OF AN AREA by an animal in order to gain more exclusive access to a contested resource. Nectarivorous birds have been the focus of a large body of work on the economics of territory defense (*e.g.,* Gill & Wolf 1975, Carpenter & MacMillen 1976, Ewald & Bransfield 1987, Heinemann 1992). These birds are model organisms for such studies because their territories are small, their energetic demands are high, and their food resources are easy to quantify and manipulate. Thus, many of the potential costs and benefits of territory defense in these species have been well studied. In this paper, I present information on two aspects of interspecific territory defense that have received relatively little attention.

First, I examine the influence of intruder size on defense behavior. Larger individuals may be more willing to engage in escalated contests over a resource (Krebs & Davies 1993, pp. 150–164), which could result in costs to the territory holder, such as increased energy expenditure and risk of injury (Gill & Wolf 1975, Kodric-Brown & Brown 1978, Ewald 1985) or increased risk of predation while involved in the contest (Jakobsson *et al.* 1995).

Second, I test for an influence of territory quality on defense behavior. This issue has been the subject of numerous studies (*e.g.*, Kodric-Brown & Brown 1978, Hixon *et al.* 1983, Powers & McKee 1994), but manipulations of territory quality frequently have been carried out with artificial feeders, which alter the perception of the resource value by both the territory holder and the potential intruders (but see Ewald & Carpenter 1978, Ewald & Bransfield 1987, Eberhard & Ewald 1994). Thus, observed changes in territory defense behavior in response to changes in territory quality may be

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confounded by changes in intruder behavior in many studies. In this study I manipulated the resource value of the territory in a manner that is readily perceived by a territory holder but is much less discernible to potential intruders. This study deals strictly with interspecific interactions during the non-breeding season, so food is the only resource that is being defended.

METHODS

STUDY SPECIES AND AREA.—I conducted the research at the La Selva Biological Station (McDade *et al.* 1994) during August 1992 in the Atlantic lowlands of northeast Costa Rica. I examined the territorial behavior of a tropical resident nectarivore, the rufous-tailed hummingbird (*Amazilia tzacatl*; mean mass 5.1 g for males, 4.85 g for females; F. G. Stiles, pers. comm.). I conducted behavioral observations at a single territory defended by a rufous-tailed hummingbird of unknown sex. The territory was approximately 200 m^2 and was located in the grassy clearing around the lab buildings of the biological station. The defended area contained two nonflowering trees and three flowering *Hamelia patens* (Rubiaceae). *Hamelia patens* is a short spreading treelet 5–10 m tall. Its flowers are small, with red tubular corollas, and are grouped in inflorescences containing 0–5 open flowers per day, for a total of a few hundred open flowers on a single tree on any given day. At La Selva, flowers of this species typically open just after midnight, produce nectar from just before dawn until mid-morning, and drop off the tree in late afternoon or evening of the same day (Colwell & Naeem 1994, Newstrom *et al.* 1994, Colwell 1995).

The four species of intruder hummingbirds that I observed are the crowned woodnymph (*Thalurania colombica*: mean mass 4.6 g, $N > 50$ for males; 4.1 g, $N > 50$ for females; F. G. Stiles, pers. comm.), the blue-chested hummingbird (*Amazilia amabilis*; mean mass 4.1 g, $N = 20$ for males; 3.7 g, $N = 24$ for females; F. G. Stiles, pers. comm.), the violet-headed hummingbird (*Klais guitmeti*; mean mass 2.95 g, $N = 15$ for males; 2.80 g, $N = 18$ for females; F. G. Stiles, pers. comm.), and the snowcap (*Microchera albocoronata*: mean mass 2.52 g, $N = 14$ for males; 2.55 g, $N = 21$ for females; F. G. Stiles, pers. comm.). These four species are sexually dimorphic in plumage, and all five study species have been observed defending territories at least occasionally (Stiles & Skutch 1989). None of these species has a breeding season that overlaps with the study period (Stiles & Skutch 1989). Territorial intrusions by other rufous-tailed hummingbirds were too infrequent to be informative and were excluded from analysis because they represent a potentially different sort of behavioral interaction.

BEHAVIORAL OBSERVATIONS.—On the mornings of 3 and 4 August 1992 ("control days"), I made behavioral observations at the territory for one 25-min period per hour, beginning at 0830 on 3 August and at 0730 on 4 August and ending at 1200 on both days. During each 25-min period, I took scan samples every minute to determine the location of the territory owner (on or off the territory), and I made continuous observations of all intrusions into the territory by other hummingbirds. Each time an intruder approached within 2 m of a defended tree, I recorded the species and sex of the intruder, the time of the intrusion, and the response of the territory owner (chase, fight, or ignore, where a fight was defined by physical contact). I used the same protocol on 7 August 1992 ("treatment day") beginning at 0730, but the resource value of the territory was experimentally manipulated during this period (see below). Because birds were not banded or marked, particular intruder individuals could not be identified.

RESOURCE QUANTIFICATION.—To quantify fluctuations in the quality of the territory between days, I estimated the total number of open *H. patens* flowers on each of the three observation days (3, 4, and 7 August). For the three *H. patens* trees on the territory, I counted the number of open flowers in an estimated one-third of each tree and multiplied by three. I counted flowers in the same portions of the trees on each day to insure repeatability. All counts were made between 1400 and 1500 h. These counts may slightly underestimate the number of flowers open earlier in the day because some flowers may drop off as early as 1200–1300 h (F. G. Stiles, pers. comm.).

RESOURCE MANIPULATION.—On 7 August, flowers in the territory were supplemented with artificial nectar to increase the resource base available to nectarivores. A suction hose and a microcapillary tube were used to inject approximately 30–40 µl of 14 percent (wt./wt.) sucrose solution into 100 flowers on the *H. patens* tree most frequently used by the territory owner for roosting and foraging. At 0900, 1000, and 1100 h, I injected the same 100 flowers, which represented nearly 20 percent of the 543 flowers open on that tree during that day.

STATISTICAL ANALYSES.—I used loglinear models to assess the effects of several categorical variables on the dichotomous response of the territory holder to intruders (chase vs. no chase). This use of loglinear models allows testing for the effect of one explanatory variable while controlling for the effects of others. In a preliminary model I used intruder SPECIES, intruder SEX, TIME of day (before or after 0900 h), and DAY (resource supplementation or control) as potential explanatory variables. Because the manipulation of resource value was initiated at 0900 h, an effect of the experimental treatment would likely appear as an interaction between treatment and time of day; thus, I included a TIME*DAY interaction term in the model also. No other interactions among predictor variables were included because they were not of biological interest.

I tested for daily variation in post-0900 intrusion pressure by comparing number of intruders per 25-min observation period on control days and treatment day using a Mann-Whitney U test. I made a second comparison in which I subdivided these 25-min periods into 5-min blocks, because intrusion events are likely to be independent over this smaller time span.

I used regression analysis to determine if the proportion of intruders that was chased in a given 25-min period was a function of the number of intrusions during that same period. This analysis was restricted to observations made on the two control days, and the proportion of intruders chased was arcsin square root transformed prior to analysis.

Finally, I used a one-way ANOVA to determine if post-0900 territory attendance differed between treatment and control days. For each 25-min observation period, I scored the number of scans (out of 25) in which the territory holder was located on the territory.

I used SAS (SAS Institute Inc. 1989) for loglinear analyses, ANOVA, and regression. SAS employs the Newton-Raphson iterative maximum likelihood method for estimating parameters in loglinear models. I used Statview (Feldman *et al.* 1988) for Chi-square and Mann-Whitney U tests. For the Chi-square tests, I used the conservative Yates continuity correction for single degree of freedom tests as recommended by Zar (1984).

RESULTS

I observed 151 behavioral interactions between hummingbirds in 5 h 50 min of observations. There were 12 interactions that were solely between two intruding individuals, 2 (16.7%) of which were fights. There were 139 interactions between intruders and the territory holder, none of which was a fight. Thus, all interactions between intruders and the territory holder were classified as either chases or non-chases. Chases were of varying duration but eventually resulted in the intruder leaving the territory, albeit sometimes only briefly. *Klois guitmeti* was the only species for which I observed intrusions by females.

The preliminary loglinear analysis of territorial interactions provided an acceptable fit to the observed data (likelihood ratio $X^2 = 5.18$, df = 24, $P = 1.00$) Only two terms significantly predicted the frequency with which intruders were chased: SPECIES ($X^2 = 12.90$, df = 1, $P = 0.005$) and the TIME*DAY interaction ($X^2 = 7.08$, df = 1, $P = 0.008$). Main effects for SEX, TIME, and DAY were not significant (all $P > 0.1$). This model was very sparse (*i.e.*, had many cells with observed frequencies = 0) due to the inclusion of SEX as a factor when female intruders were observed for only one species. Therefore, I next fit a reduced model which included only the terms that were significant in the first model: SPECIES and TIME*DAY interaction. This model also provided an acceptable fit to the data (likelihood ratio $X^2 = 7.60$, df = 11, $P = 0.748$) and did not provide a significantly poorer fit than the fuller model (difference in likelihood ratio $X^2 = 2.42$, difference in df = 13, $P = 0.995$; Agresti 1990). The terms SPECIES and TIME*DAY were still significant ($X^2 = 14.54$, df = 3, $P = 0.002$; and $X^2 = 12.80$, df = 1, $P = 0.001$, respectively). The lambda parameter estimates for the four levels of SPECIES can be interpreted as a measures of the contribution of each level of SPECIES to the probability of the intruder being chased. The rank order of the lambda estimates corresponds to the inverse rank order of species body mass (Fig. 1).

As a follow-up test, I compared the treatment day to the pooled control days both before 0900 and after 0900 h in order to determine which difference contributed to the significant TIME*DAY interaction noted in the loglinear model (Fig. 2). This Chi-square test should be interpreted cautiously because cells are collapsed across values of a variable (SPECIES) that is a significant predictor of the response of the territory holder to an intruder (Agresti 1990). The proportion of pre-0900 intruders chased did not differ between treatment day and the two control days pooled ($X^2 = 1.85$, df = 1, $P = 0.174$). The proportion of post-0900

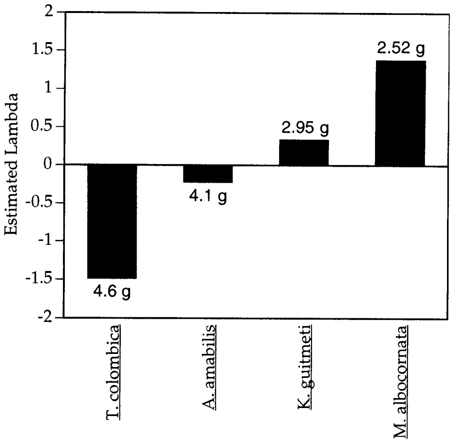

FIGURE 1. Estimated values of lambda from a loglinear model of factors affecting the probability of an intruder being chased by the territory holder. The magnitude and sign of lambda for a given intruder species are indicative of the extent to which intruders of that species are likely to be chased by the territory holder when controlling for the effects of other factors (positive sign more likely to be chased, negative sign less likely to be chased). Numbers above or below the bars are mean body mass values for males of each species.

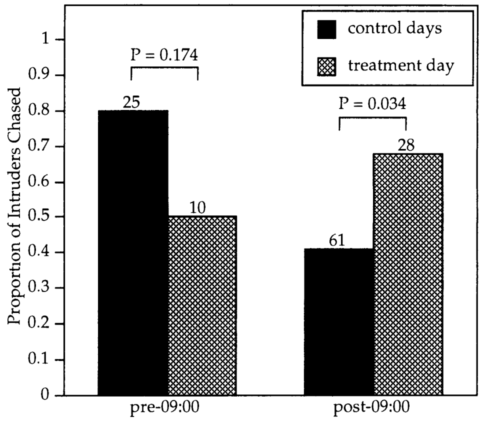

FIGURE 2. Proportion of intruders chased from the territory by the resident *Amazilia tzacatl* on control days and on the day when the resource value of the territory was experimentally supplemented. Comparisons are made separately for observations before and after 0900 h, the time at which nectar supplementation was begun on the treatment day. Numbers above bars indicate the total number of interactions between the territory holder and heterospecific intruders. P-values are based on Chi-square tests as reported in the text.

intruders chased was significantly greater on the treatment day than on the control days pooled ($X^2 = 4.52$, df = 1, $P = 0.034$). This suggests that the significant TIME*DAY interaction is due to the high proportion of intruders chased following nectar supplementation.

I carried out several additional analyses in order to determine whether other factors could have been responsible for the high proportion of chases observed after 0900 on the day of resource supplementation. I first tested for daily variation in intrusion pressure and whether this could affect territory defense behavior. There was no difference between control days and treatment day in the number of post-0900 intruders per 25-min period (Mann-Whitney U test, $N^1 = 6$, $N^2 = 3$, U = 9, $P = 1.0$). There was also no difference if observations were subdivided into 5-min periods ($N_1 = 30$, $N_2 = 15$, U = 225, $P = 1.0$). Over the two control days, there was no linear relationship between the proportion of intruders chased and the frequency of intrusions ($F1,7 = 0.594$, $P = 0.466$, $r^2 = .0783$).

Second, because territory defense is contingent upon the presence of the territorial bird, I compared post-0900 territory attendance between the treatment day and the two control days. There was no difference in the number of scans in which the territory holder was located on the territory (one-way ANOVA, $F_{1,7} = 0.16$, p = 0.700).

Finally, I compared a coarse measure of natural resource availability on the control days and the treatment day. The estimated number of open flowers on the territory was higher on the treatment day (1045 for all three trees) than on either of the two control days (864 and 885 for days 1 and 2, respectively). Similarly, the estimated number of open flowers on the experimental tree was 421, 372, and 543 for days 1, 2, and 3, respectively.

DISCUSSION

EFFECTS OF INTRUDER IDENTITY.—I found significant variation among the four intruder species in their likelihood of being chased by the territory holder. I evaluate five hypotheses which pertain to interspecific variation in the likelihood of an intruder being chased by a territorial bird. A 'risk of takeover' hypothesis predicts that a territorial bird should be most aggressive towards intruders that pose the greatest threat of taking over the territory. In the case of this study, all four intruder species are territorial at least occasionally (Stiles & Skutch 1989), but only *A. amabilis* and *T. colombica* defend territories at *H. patens* trees (F. G. Stiles, pers. comm.). Thus, these two species should be chased more frequently (i.e., have larger, positive lambda values in the loglinear model) than *M. albocoronata* and *K. guitmeti.* The observed results do not support this prediction (Fig. 1).

A second hypothesis relates agonistic interactions to the wing disc loading of the contestants. Wing disc loading (L_{WD}) is the ratio of a bird's body mass to the area of the disc swept out by the wings during flight. High L_{WD} provides the benefit of increased high-speed maneuverability but entails a greater energetic cost for hovering (Feinsinger & Chaplin 1975). Territorial hummingbirds frequently have higher L_{WD} than traplining species (Feinsinger & Chaplin 1975). Increased maneuverability may enhance a bird's ability to defend a territory, and increased cost of hovering could be offset by a reduction in the amount of time spent hovering relative to a trapline-foraging bird. Studies of several hummingbird communities have supported this relationship between high L_{WD} and territorial behavior or likelihood of winning aggressive encounters (Feinsinger & Chaplin 1975, Feinsinger & Colwell 1978, Feinsinger *et al.* 1979, Carpenter *et al.* 1993). However, the hummingbird community at La Selva does not appear to fit this pattern. For the hummingbirds at La Selva, Stiles (1995) found that wing disc loading was related to mode of arthropod foraging but not to mode of nectar foraging. Stiles (1995) also presented calculations of L_{WD} for *A. tzacatl, A. amabilis,* and *T. colombica,* giving values based on two different equations which use either wing chord or total wing length to estimate wing span. By either measurement, *A. tzacatl* had the highest L_{WD} and thus should be the most maneuverable and the most likley to win an aggressive contest. This is not consisent with the low frequency with which I observed the territorial *A. tzacatl* initiate chases against *T. colombica* intruders, which have a lower L_{WD}.

A third hypothesis, 'intruder detectability,' proposes that small intruders may be more difficult for the territory holder to detect (*e.g.,* 'filchers' of Feinsinger & Colwell 1978) and thus would be chased less frequently. Among the four intruder species that I observed, the smallest ones were actually most likely to be chased (Fig. 1).

A fourth hypothesis proposes that the frequency with which an intruder is chased depends upon its potential for resource removal. It may be more important to chase intruders that are morphologically capable of removing large quantities of nectar. Interspecific variation in bill morphology can result in differences in effectiveness of nectar removal (Wolf *et al.* 1976). Although *A. tzacatl* and the four intruder species all have relatively straight bills (Stiles & Skutch 1989), the length of the exposed culmen ranges from 11–12.5 mm for *M. albocoronata* to 20.5–23.0 mm for *A. tzacatl* (F. G. Stiles, pers. comm.). The effective corolla length (distance from the distal end of the corolla to the distal end of the nectar chamber in the base of the corolla) of *H. patens* flowers at La Selva is 15.6 ± 1.7 mm (N = 20; F. G. Stiles, pers. comm.). Daily nectar production often exceeds the volume of the nectar chamber such that a bird with a bill slightly shorter than 15 mm would be able to access at least some of the nectar in many flowers (F. G. Stiles, pers. comm.). However, the smaller-billed intruders such as *M. albocoronata* and *K. guitmeti* are probably unable to access all of the nectar in *H. patens* flowers. The 'potential for resource removal' hypothesis predicts that these two species should be chased least frequently because their intrusions are less likely to result in substantial resource removal. The observed data do not support this prediction (Fig. 1).

A final potential explanation for the observed interspecific variation in tendency to be chased is a 'cost of engagement' hypothesis. This hypothesis argues that intruders should be chased in accordance with the potential costs associated with engaging them in aggressive contests. Risk of injury to the territory holder may be low since hummingbirds rarely engage in physically dangerous fights (but see Kodric-Brown & Brown 1978), but several other costs may be related to intruder size. Interactions between contestants closely matched in body size may be more likely to escalate into protracted contests (Krebs & Davies 1993, pp. 160–164), which could lead to increased risk of predation during the contest (Jakobsson *et al.* 1995) and which would also increase the energy expenditure of the contestants (Ewald 1985). The 'cost of engagement' hypothesis predicts that the frequency with which intruders are chased should vary inversely with intruder body size. This prediction is supported by the lambda values from the loglinear analysis (Fig. 1). However, this hypothesis would also predict that *K. guitmeti* males would be chased less frequently than females since males are slightly heavier. I did not detect a difference between male and female *K. guitmeti* in their tendency to be chased. However, the size difference is slight, and a sex-based difference in aggressive behavior by *A. tzacatl* might only be detected with a larger number of behavioral observations.

Although other interpretations are possible, it appears that the response of the territorial *A. tzacatl* to an intruding individual depends in part on the intruder's size. This is consistent with the relationship between size and probability of winning agonistic enounters that has been noted in other hummingbird communities (Stiles & Wolf 1970, Feinsinger 1976, Lyon 1976, Feinsinger & Colwell 1978).

EFFECTS OF RESOURCE MANIPULATION.—The intensity of territory defense, as measured by the proportion of intruders chased by the territory holder, was higher during the period of resource supplementation than at the same time on the two control days (Fig. 2). Although there were more flowers open on the territory on the treatment day than on the control days, this difference was probably not responsible for the observed difference in the proportion of post-0900 intruders chased. The treatment day did not differ from the control days in the proportion of pre-0900 intruders chased by the territory holder (Fig. 2). This suggests that the difference between treatment and control days in post-0900 chase behavior was due to my resource manipulation rather than to other intrinsic differences between the days, such as natural resource availability. In addition, I found no differences in intrusion pressure or territory attendance which would offer alternate explanations for the difference between treatment and control days in post-0900 chase behavior. Thus, the observed increase in territory defense appears to be a result of the experimental increase in the resource value of the territory.

This interpretation—that resource supplementation caused the observed change in territorial behavior—is supported by a previous study of nectar production and removal at *H. patens* trees at this same study site. Colwell (1995) measured nectar content in three classes of *H. patens* inflorescences: control flowers which were unmanipulated, flowers from which hummingbirds had been excluded, and flowers from which both hummingbirds and the hummingbird flower mite *Proctolaelaps kirmsei* had been excluded. By early morning (0730–0900), the unprotected control flowers contained an average of only 1.5 μl of nectar–86 percent less than flowers from which both birds and mites had been excluded. At this point in the morning, the nectar consumed by hummingbirds and mites will not be replenished because *H. patens* nectar production ceases at La Selva by approximately 0900 (Colwell & Naeem 1994, Newstrom *et al.* 1994). Thus, for a hummingbird defending a territory of *H. patens,* the value of the resource is greatly reduced by 0900, and rufous-tailed hummingbirds are presumably capable of monitoring the resource value of their territories, as has been demonstrated for a Costa Rican congener, *A. saucerottei* (Trombulak 1990). At Monteverde, *A. saucerottei* and *A. tzacatl* individuals defending *H. patens* trees frequently abandoned their territories as the day progressed, presumably in response to depletion of nectar following the midmorning cessation of nectar production (Feinsinger 1976). Therefore, in the current study, it seems probable that experimental nectar supplementation increased the value of the territory at a time when the resource base was depleted, this change was detected by the territory holder, or the territory holder responded by increasing the intensity of territory defense.

Many previous studies have shown changes in territorial behavior in response to alterations of resource value. Studies have demonstrated both upper and lower limits to economic defensibility (*e.g.,* Carpenter & MacMillen 1976), as well as changes in the manner in which defense is carried out (*e.g.,* chases vs. displays; Ewald & Carpenter 1978, Ewald & Bransfield 1987). However, most of these studies have not controlled for changes in intruder behavior that may parallel the changes in resource value. For instance, if the resource value is altered by pruning flowers or adding artificial feeders, this change in value is probably apparent to potential intruders before they actually enter the territory. Thus, an increase in resource value may spur an increase in intruder pressure (Marchesseault & Ewald 1991) which can cause an increase in territorial defense intensity (Tamm 1985). In this study, I altered the territory holder's perception of the resource value while minimizing changes in intruder behavior. By doing so, I found that territorial *A. tzacatl* can increase its intensity of defense purely in response to an increase in the value of its territory. I do not know whether this response would reach an upper threshold at which territory defense would be discontinued due to its unprofitability. Although limited in scale, this study provides two important conclusions that are relevant to our understanding of interspecific territoriality: decisions about whether to defend against a particular intruder may be based, in part, on intruder body size; and short-term decisions about territory defense intensity can be contingent upon resource value, independent of changes in intruder pressure.

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