

Does interspecific territoriality reflect the intensity of ecological interactions? A theoretical model for interspecific territoriality

Osamu K. Mikami^{1*} and Masakado Kawata²

¹*Department of Ecology and Evolutionary Biology, Biological Institute, Graduate School of Science and* ²*Division of Ecology and Evolutionary Biology, Graduate School of Life Sciences, Tohoku University, Aoba-ku, Sendai 980-8578, Japan*

ABSTRACT

In many studies, interspecific territorial behaviours among co-existing species have been used to infer the presence and the intensity of underlying ecological interactions between species, mainly resource competition. However, the theoretical background of this inference is insufficient. Hence, we constructed a simple theoretical model of interspecific territoriality assuming that interspecific territorial defence is the optimal behaviour. We discuss the factors promoting interspecific territoriality and the relationship between interspecific territoriality and ecological interactions. The model predicts that: (1) a territory holder preferentially excludes intruders of species with high 'exclusion efficiency'; (2) the decision by the territory holder to exclude a certain species or not does not depend on the probability of finding intruders of the species or on the number of intrusions by the species; and (3) interspecific territoriality does not always reflect the intensity of ecological interactions between species. These results indicate that the observation of interspecific territoriality does not necessarily indicate the intensity of ecological interactions. In addition, if territory holders defend their territories as predicted by the present optimal model, the co-existence of competing species is promoted.

Keywords: ecological interaction, foraging theory, theoretical model, interspecific competition, interspecific territoriality, optimal behaviour, species co-existence.

INTRODUCTION

Some animals defend their territories not only against conspecific individuals (intraspecific territoriality), but also against heterospecific individuals (interspecific territoriality). Interspecific territoriality has been observed, for example, in ants, fishes and birds (Murray, 1981). There has been some debate about the cause of interspecific territoriality (Wiens, 1989; Krebs and Davis, 1993). Murray (1971, 1976, 1981) suggested that interspecific territoriality arises when a territory holder merely misidentifies heterospecific intruders

* Address all correspondence to Osamu Mikami, Department of Biology, Faculty of Science, Kyushu University, 6-10-1 Hakozaki, Higashi-ku, Fukuoka 812-8581, Japan. e-mail: omikascb@mbbox.nc.kyushu-u.ac.jp
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as conspecifics and thus interspecific territoriality is not directly related to ecological interactions among species. Others (Orians and Willson, 1964; Cody, 1969, 1973, 1974; Low, 1971; Catchpole, 1977, 1978; Ebersole, 1977; Lyon *et al.*, 1977; Davies, 1978) have claimed that individuals defend their territories against both conspecific and heterospecific individuals, since they can gain benefits by defending their resources (e.g. food supplies, shelters and breeding sites) and/or their eggs.

Many detailed studies (Kohda, 1981, 1998; Reed, 1982; Catchpole and Leisler, 1986; Prescott, 1987; Robinson and Terborgh, 1995; Martin *et al.*, 1996; Genner *et al.*, 1999; Martin and Martin, 2001a,b) have favoured the latter view. That is, they indicated that interspecific territorial behaviour is an adaptive behaviour, but is not caused by the misidentification of species. For example, the observation that territory holders exclude heterospecific intruders whose size and/or colour patterns are strikingly different from those of conspecific intruders (e.g. Reed, 1982; Martin *et al.*, 1996) indicates that species misidentification is not adequate as a general explanation for interspecific territoriality.

In the above studies, interspecific territorial behaviours among co-existing species have been used to infer the presence and the intensity of underlying ecological interactions between species, mainly resource competition. When researchers observed that individuals of a certain species defended their territories against heterospecific intruders, they tended to believe that there was an ecological interaction between the two species. More precisely, when researchers observed that a certain territorial species A defended its territory against species B not but species C, they tended to conclude that the intensity of ecological interactions between species A and B was stronger than that between species A and C.

However, is this inference – namely, that interspecific territoriality reflects the intensity of ecological interactions – actually correct? Factors other than the intensity of ecological interactions would affect the occurrence of interspecific territoriality. For instance, the decision by territory holders to exclude intruders of a certain species might depend on the frequency of the intrusions, the cost of excluding the intruders and the probability of finding the intruders. If these factors have an influence on interspecific territoriality, the inference might not always be correct. In particular, if individuals of a certain species preferentially intrude into the territory of individuals of an ecologically similar species because they gain more benefit from their territories, and if territory holders preferentially exclude individuals of a species that intrudes into the territory more frequently, researchers can easily draw the wrong conclusion. Thus, interspecific territoriality might not reflect the intensity of ecological interactions.

To try to answer these questions, we present a simple theoretical model for interspecific territoriality. To date, no detailed theoretical studies on interspecific territoriality have been conducted. Therefore, there has been a lack of theoretical discussion on interspecific territoriality and the inference that interspecific territoriality reflects the intensity of ecological interactions has thus been accepted without a clear theoretical background. Hence, a theoretical study on interspecific territoriality is of great importance.

In the present model, we assume that territory holders behave to maximize fitness per time by defending their benefits (e.g. resources, eggs and mating opportunities) against conspecific and heterospecific intruders. That is, we assume that intraspecific and interspecific territorial defence is an optimal adaptive behaviour. Based on this theoretical analysis, we discuss which factors promote interspecific territoriality and the relationship between interspecific territoriality and the intensity of ecological interactions. Such a discussion may have important implications for the interpretation of interspecific territoriality and its evolution.

THE MODEL

The equations employed in the present model are similar to those of the optimal foraging model of Charnov (1976). The optimal foraging model predicts how many items a predator should add to its diet by assuming that a predator behaves to maximize energy intake per time. Similarly, by assuming that a territory holder behaves to minimize the total cost of territorial defence and damage suffered from intrusion per time, the present model predicts how many species will be defended against and how often a territory holder will have to defend its territory.

In the present model, we assume that there are n species. Individuals of these n species, randomly and independently of one another, intrude into the territory of a territory holder. One of these n species is a conspecific of the territory holder. The territory holder and intruders are assumed to have the following characteristics:

1. The territory holder searches for individuals which intrude into its territory (we call these individuals 'intruders'). When the territory holder finds an intruder, it can exclude or tolerate the intruder. When the territory holder chooses to exclude the intruder, it always excludes the intruder from its territory (we do not assume that intruders usurp the territory).
2. The territory holder sometimes fails to find intruders during the period of searching.
3. The territory holder finds only one intruder at a time.
4. The territory holder can exclude only one intruder at a time and this exclusion time is unavailable for searching for other intruders.
5. When an intruder is not found by the territory holder (we call it 'successful intrusion'), the intruder can copulate with a female(s) (only when the intruder is conspecific) and/or gain resources contained in the territory (when the intruder is conspecific or heterospecific). Consequently, by successful intrusion, the territory holder loses some degree of fitness.
6. The territory holder incurs no costs for recognizing intruders (i.e. time and energy).
7. The territory holder incurs costs for searching and excluding (i.e. time, energy and the risk of predation). These costs differ depending on the intruder species.
8. The territory holder behaves to minimize the fitness loss during the period of vigilance. More precisely, the territory holder behaves to minimize the total cost of searching and excluding, and the fitness loss suffered from successful intrusions by intruders per time.
9. The territory holder has complete information about the frequency of intrusions of each species.

An equation giving the fitness loss of a territory holder is derived as follows. Let E be the fitness loss of the territory holder when the territory holder excludes intruders during a period of vigilance of length T_v , which consists of T_s (time searching) and T_e (time excluding intruders). L is the fitness loss of the territory holder suffered from successful intrusions during T_v . C is the fitness loss of the territory holder resulting from searching for intruders during T_v .

Thus, R , the total fitness loss of the territory holder during T_v , is

$$R = \frac{E + L + C}{T_v} = \frac{E + L + C}{T_s + T_e} \quad (1)$$

T_e , E , L and C can be described as follows:

$$T_e = T_s \sum_{i=1}^n p_i q_i \lambda_i h_i \quad (2)$$

$$E = T_s \sum_{i=1}^n p_i q_i \lambda_i e_i \quad (3)$$

$$L = T_e \times \sum_{i=1}^n \lambda_i l_i + T_s \sum_{i=1}^n (1 - p_i q_i) \lambda_i l_i \quad (4)$$

$$C = T_s c \quad (5)$$

where each species i has the following characteristics: λ_i is the number of times that the territory is intruded by species i in one unit of vigilance time ($0 < \lambda_i$), e_i is the expected fitness loss of the territory holder necessary for the exclusion of an individual of species i ($0 < e_i$), l_i is the expected fitness loss suffered from successful intrusion by an intruder of species i ($0 < l_i$), h_i is the expected time needed by the territory holder to exclude an intruder of species i ($0 < h_i$), p_i is the probability that the territory holder finds an intruder of species i ($0 \leq p_i \leq 1$), and q_i is the frequency that the territory holder takes action against an intruder of species i when it finds one ($0 \leq q_i \leq 1$). Only q_i is controlled by the territory holder. The first term on the right-hand side of equation (4) shows the fitness loss of the territory holder suffered from successful intrusions by individuals of n species during T_e – that is, the time spent by the territory holder in excluding other intruders. The second term shows the fitness loss of the territory holder when the territory holder does not exclude intruders because it does not find them and because, even if it finds them, it chooses to tolerate them. Here, we assume that a higher value of l reflects a greater degree of niche overlap between the territory holder species and an intruder species, because an intruder species with a greater degree of niche overlap would consume a greater amount of resources necessary for the territory holder.

Then, R can be written as

$$R = \frac{T_s \sum_{i=1}^n p_i q_i \lambda_i e_i + T_s \sum_{i=1}^n p_i q_i \lambda_i h_i \times \sum_{i=1}^n \lambda_i l_i + T_s \sum_{i=1}^n (1 - p_i q_i) \lambda_i l_i + T_s c}{T_s + T_s \sum_{i=1}^n p_i q_i \lambda_i h_i}$$

or

$$R = \frac{\left(1 + \sum_{i=1}^n p_i q_i \lambda_i h_i\right) \times \sum_{i=1}^n \lambda_i l_i - \sum_{i=1}^n p_i q_i \lambda_i (l_i - e_i) + c}{1 + \sum_{i=1}^n p_i q_i \lambda_i h_i} \quad (6)$$

The territory holder should behave to minimize this R .

In the model, we assume that R is always smaller than the fitness loss of a ‘non-territorial’ individual that does not search for any intruders and does not defend its territory against any intruders (i.e. the values of q for any species i and the value of c are zero in equation (6)), because, if this were not the case, the territorial behaviour would not be adaptive. In this case, equation (6) becomes the second term on the left-hand side of equation (7). We therefore assume in the present model that the following inequality is always satisfied:

$$R - \sum_{i=1}^n \lambda_i l_i = \frac{c - \sum_{i=1}^n p_i q_i \lambda_i (l_i - e_i)}{1 + \sum_{i=1}^n p_i q_i \lambda_i h_i} < 0 \tag{7}$$

Moreover, in the model, we assume that R is not so large. When the value of R , the total fitness loss per time, is very large, the territory holder does not gain any benefit by territorial defence. In this case, the territory holder should abandon the territory and move elsewhere. Therefore, in this model, we assume that R is not so large that a territory holder should abandon its territory.

We also assume that the territory holder does not change the size of its territory. If we assume that the territory holder can change its territory size, its optimal behaviour is to maximize ‘ $F - R$ ’, where F is a function of fitness depending on its territory size (the values of parameters in R , such as p and q , are also varied depending on the territory size). However, this assumption does not affect the following qualitative discussion. This model can predict how often, how many and against what species the territory holder should exclude intruders in an arbitrary territory size.

ANALYSIS OF THE MODEL

How often should the territory holder exclude intruders?

Equation (6) has the form of a multi-species version of the Holling disk equation (Holling, 1959) and the technique for calculating the value of q when R is minimized is as follows. In equation (6), the only thing that a territory holder can control is the value of q_i . We here ask, how often should the territory holder exclude intruders of a certain species k to minimize R ? The problem of finding the optimal q_k (q_k^*) can be solved by differentiating R with respect to q_k , which yields

$$\frac{\partial R}{\partial q_k} = \frac{p_k \lambda_k \left[-(l_k - e_k) \left(1 + \sum_{\substack{i=1 \\ i \neq k}}^n p_i q_i \lambda_i h_i \right) + h_k \left\{ \sum_{\substack{i=1 \\ i \neq k}}^n p_i q_i \lambda_i (l_i - e_i) - c \right\} \right]}{\left(p_k q_k \lambda_k h_k + 1 + \sum_{\substack{i=1 \\ i \neq k}}^n p_i q_i \lambda_i h_i \right)^2} \tag{8}$$

Then, when $\partial R/\partial q_k < 0$,

$$\frac{l_k - e_k}{h_k} > \frac{\sum_{\substack{i=1 \\ i \neq k}}^n p_i q_i \lambda_i (l_i - e_i) - c}{1 + \sum_{\substack{i=1 \\ i \neq k}}^n p_i q_i \lambda_i h_i} \quad (9)$$

and hence the optimal exclusion effort q_k must be its maximum: $q_k^* = 1$. On the other hand, when $\partial R/\partial q_k > 0$,

$$\frac{l_k - e_k}{h_k} < \frac{\sum_{\substack{i=1 \\ i \neq k}}^n p_i q_i \lambda_i (l_i - e_i) - c}{1 + \sum_{\substack{i=1 \\ i \neq k}}^n p_i q_i \lambda_i h_i} \quad (10)$$

and hence the optimal exclusion effort must be zero: $q_k^* = 0$.

Thus, the optimal exclusion effort q_k^* that minimizes R is either zero or one. This indicates that the territory holder should either exclude or tolerate 'all' intruders of species i when it finds them. Equations (9) and (10) also indicate that the territory holder should exclude intruders of species with a large value of $(l - e)/h$ and should not exclude intruders of species with a small value of $(l - e)/h$. In other words, the territory holder reduces its fitness loss, or increases its fitness, by excluding intruders of species with a large value of $(l - e)/h$.

How many species should the territory holder exclude?

Here, we rank species k by the value of $(l - e)/h$ – that is, $(l_k - e_k)/h_k > (l_{k+1} - e_{k+1})/h_{k+1}$. The value of $(l_k - e_k)/h_k$ indicates an index of the efficiency of reduction of fitness loss by excluding intruders of species k . We call this $(l - e)/h$ 'exclusion efficiency'. The territory holder should preferentially exclude intruders of species with high exclusion efficiency.

By ranking species by $(l - e)/h$, equation (9) can be described as follows:

$$\frac{l_k - e_k}{h_k} > \frac{\sum_{i=1}^{k-1} p_i \lambda_i (l_i - e_i) - c}{1 + \sum_{i=1}^{k-1} p_i \lambda_i h_i} \quad (11)$$

The territory holder should exclude intruders of species 1 to species k as long as this equation (11) is satisfied. Equation (11) also indicates that whether the territory holder should exclude intruders of species k does not depend on the values of p_k and λ_k .

Conditions under which the territory holder excludes only conspecific intruders

It is important to clarify the conditions under which the territory holder defends its territory against only conspecific intruders (only intraspecific territoriality) or against both conspecific and heterospecific intruders (interspecific territoriality). From equation (11), the condition for which the territory holder defends its territory against only one species is as follows:

$$\frac{l_2 - e_2}{h_2} < \frac{p_1 \lambda_1 (l_1 - e_1) - c}{1 + p_1 \lambda_1 h_1}$$

or

$$(l_2 - e_2) + h_2 c + p_1 \lambda_1 \{h_1(l_2 - e_2) - h_2(l_1 - e_1)\} < 0 \quad (12)$$

In equation (12), $h_1(l_2 - e_2) - h_2(l_1 - e_1) < 0$ because we assume that $(l_1 - e_1)/h_1 > (l_2 - e_2)/h_2$. Here, we assume that species 1 is a conspecific of the territory holder. The l of such a conspecific would be much larger than that of a heterospecific species because the niche overlap between conspecifics is greater and because the conspecific intruder may perform extra-pair copulations. Therefore, this assumption is reasonable. Thus, equation (12) means that the territory holder defends its territory against only conspecific intruders when the value of $(l - e)/h$ of conspecific intruders is much larger than that of heterospecific intruders and the value of $p \times \lambda$ of conspecific intruders is large. The latter condition indicates that when the number of conspecific intruders is sufficiently large, the territory holder should defend its territory against only conspecific intruders. Note that species 1 must satisfy the condition, $l_1 - e_1 > c/p_1 \lambda_1$, which is derived from equation (7).

If we assume species 1 is a heterospecific intruder of the territory holder, the territory holder excludes preferentially heterospecific intruders rather than conspecific intruders. However, no study has reported such a case and thus it is unlikely. Perhaps, this case may apply to species that breed in colonies because they do not exclude conspecifics but exclude natural enemies. However, that situation is different from this model and thus is not considered here.

DISCUSSION

How often do territory holders exclude a certain species?

The present theoretical model predicts that the value of q should be either zero or one. This means that territory holders should exclude or tolerate all intruders to maintain an efficient defence when they find intruders of a certain species. This prediction has not been derived from any previous models. Unfortunately, to our knowledge, there are no data to either support or refute this prediction.

However, in nature, contrary to predictions, territory holders might exclude not all but only a portion of intruders because they may not have complete information about the frequency of intrusions by each species (although in the model the territory holder is assumed to have complete information). Moreover, even if territory holders have complete information, they may recognize intruders by the intruders' appearance such as colour and size (e.g. Kohda, 1981), and thus they may exclude all intruders of the same appearance.

As a result, the territory holders might not exclude all intruders of the same species within which there are individual variations in colour and size.

Conditions that promote interspecific territoriality

From equations (11) and (12), the conditions that promote interspecific territoriality are that the $(l - e)/h$ of heterospecific intruders is high and/or the value of $p \times \lambda$ of conspecific intruders is not so large. This means that territory holders should exclude heterospecific intruders as well as conspecific intruders when the exclusion efficiency of the heterospecific intruder is high and/or when they cannot sufficiently exclude conspecific intruders and they waste time in searching for intruders. Therefore, if the values of $p \times \lambda$ of the conspecifics decrease in proportion to the increase in the number of species in a local community, then interspecific territoriality is likely to occur. This prediction is more plausible than that of Orians and Willson (1964), who predicted that interspecific territoriality may be promoted when environmental features restrict ecological divergence.

These theoretical consequences of the conditions that promote interspecific territoriality can explain the field observations that fish species tend to exclude a greater number of species than do birds (see Low, 1971; Murray, 1981). In most bird species, the damage caused by intrusion by conspecific individuals will be greater than that caused by heterospecific individuals, because the most important reason for territorial defence is to prevent intruders from mating with the territory holder's female(s). Therefore, in many bird species, individuals tend mainly to defend their territories against conspecific intruders. On the other hand, for fish species, because the protection of nest sites and eggs are important functions of territorial defence (Ebersole, 1977), the damage resulting from intrusion by conspecific intruders is not that different from that caused by heterospecific intruders. Therefore, in many fish species, individuals defend their territories against heterospecific intruders as well as against conspecific ones. Moreover, in fish communities, particularly tropical reef fish communities, many species co-exist in a local area, and the densities of conspecifics are lower than those in communities with few species. Therefore, interspecific territoriality may be likely to occur in many fish species.

Against what species should territory holders defend?

From equation (11), the decision by a territory holder to exclude a certain species (species k) depends on the value of $(l - e)/h$ of that species but not on the values of p and λ of that species. Also, the decision depends on the parameters of other species (species 1 to species $k - 1$) which the territory holder should preferentially exclude. This means that the territory holder should exclude intruders of species which he can exclude at low cost (e) and in a short time (h), and species whose intrusion causes the territory holder to lose much fitness (l). But the decision is independent of the probability of finding the species (p) and the number of intrusions by that species (λ).

These predictions suggest that territory holders do not always defend their territories against heterospecific intruders occupying a similar niche, since the model predicts that the territory holder excludes species with a high value of $(l - e)/h$ but not necessarily with a high value of l (as described in the model, the value of l reflects the degree of niche overlap between the territory holder species and a certain intruder species). For example, when the territory holders are the dominant species in aggressive encounters against individuals of a

certain heterospecific intruder and can easily exclude them, they defend their territories against those intruders even if the degree of niche overlap is not so large. Indeed, such territorial behaviours have been observed in several studies (see Murray, 1981).

These predictions are more plausible than that of Cody (1974). Cody predicted that individuals defend their territories against species with which diet overlap is high. This diet overlap is similar to the value of l in our model. Although the value of l of a certain species would influence the decision of territorial defence against that species, it would not be sufficient on its own.

Does interspecific territoriality reflect the intensity of ecological interactions?

As described above, interspecific territoriality does not always reflect the intensity of ecological interactions between species (e.g. resource competition). However, many studies (Kohda, 1981, 1998; Reed, 1982; Catchpole and Leisler, 1986; Prescott, 1987; Robinson and Terborgh, 1995; Martin *et al.*, 1996; Genner *et al.*, 1999; Martin and Martin, 2001a,b) have indicated that interspecific territoriality is evidence for the intensity of ecological interactions. Of course, there will be some cases when interspecific territorial defence behaviour actually results from strong ecological interactions (e.g. Martin and Martin, 2001a,b), but it is incorrect to consider all interspecific territoriality as evidence of the intensity of ecological interactions. Therefore, we should be cautious when we interpret the relationships between the intensity of ecological interactions and the existence of interspecific territoriality.

Interspecific territoriality and species co-existence

One of the most interesting questions in ecology is whether interspecific competition between species causes the exclusion of one species or results in co-existence. It has been suggested that under interspecific competition, several mechanisms, including environmental heterogeneity, predation, disturbance, co-evolution and niche differentiation, can promote co-existence (Begon *et al.*, 1996). The present model provides an additional mechanism that promotes species co-existence. Assume two competing species, A and B, both of which share a similar niche. When the population size of species A increases, the individuals of species A defend their territories against only conspecific intruders according to the present model. At that time, the negative effect from species A on species B becomes weak and species B will have high reproductive success. In this way, a species with a smaller population size always has a high growth rate. Consequently, two competing species can co-exist. Murray (1981) claimed that, as a result of interspecific territoriality, subordinate species become extinct or evolve to shift their niche through aggression by a dominant species. Contrary to Murray's explanation, our proposed mechanism promotes species co-existence without a niche shift. Thus, adaptive interspecific territorial behaviour could lead to species co-existence. The present mechanisms for species co-existence should be tested in future work.

CONCLUSION

The theoretical model presented here provides several implications and predictions for the causes, consequences and evolution of interspecific territoriality. The present results

indicate that we should be careful when interpreting the ecological significance of interspecific territoriality, for example the observation that interspecific territoriality does not necessarily indicate the intensity of interspecific competition.

The present model also implies that adaptive behaviour may change the intensity of interspecific competition (that is, the competition coefficient in the Lotka-Volterra model) and, consequently, may lead to species co-existence. As indicated by Orians (2000), the influence of behaviour on the structure of an ecological community may play an important role in ecology and ethology.

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