Territory Area as a Determinant of Mating Systems[1]

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SYNOPSIS. Territoriality is an integral part of breeding behavior in many animals. Because the reproductive success of territorial males is often limited by access to females, breeding males should behave as "area maximizers" when the basis of female choice is either the abundance of resources within the territory or territory area per se. Being reproductively more limited by energy, territorial females should be "energy maximizers." A series of simple analytical models of territory area for such foragers is developed to explore how changes in local food production and/or local competitor density affect both the probability of a territorial male securing more than one mate (polygyny) and the probability of his and his mates' reproductive success increasing. Two cases are modeled (only males territorial vs. both sexes territorial), each for various sets of assumptions regarding interactions between food production, feeding efficiency, and competitor density. Concurrent responses in territory area, territory food reserves, net energy gain, and time budgeting provide testable sets of predictions for each scenario. Where only males are territorial (Case I), changes in food production can have different (indeed, opposite) effects upon an individual male's probability of becoming polygynous, depending upon whether the basis of female choice is the abundance of food within the territory or another factor positively correlated with territory area. Increases in competitor density usually decrease the probability of polygyny regardless of the basis of female choice. Where both sexes are territorial and territories overlap intersexually (Case II), the mating system becomes a function of the number of female territories within each male's territory, which varies with the ratio of male to female territory areas. In this case, the probability of polygyny occurring will increase if food production for both sexes increases without concurrent increases in competitor density, and will decrease if competitor density for both sexes increases without concurrent increases in feeding efficiency. Few data are presently available to test either these general predictions or numerous sets of secondary predictions tabulated in the text. Available evidence is largely consistent with the models, but mostly circumstantial. This is because the predictions of these and other models of territory area are strongly assumption dependent, and few published studies have investigated these assumptions. These analyses demonstrate that to accurately assess the mechanisms by which environmental factors affect territory area, and thus mating systems, tests of the underlying assumptions of models are essential.

INTRODUCTION

Feeding territoriality, in the general sense of an animal defending its foraging area (which may include other resources), is an integral part of breeding behavior in many species. Most field studies have focused on two breeding situations involving feeding territories. In the first (hereafter, Case I), only males are territorial. At the onset of the breeding season, females distribute themselves among territories, so the mating system depends upon the number of breeding females settling in each male's territory. In the second situation (Case II), both sexes defend individual territories. Here, the mating system depends upon the number of female territories included within each male's territory. In both situations, a polygynous mating system results when a male secures two or more mates.

This paper explores how factors affecting territory area might influence the mating system and reproductive success of individuals in both of the above situations. I do not propose that territory area is the most important determinant of mating systems; obviously, many interacting factors are involved (Vehrencamp and Bradbury, 1984). My goal is to examine the role of this particular factor. My approach extends a set of simple analytical models originally designed to predict how changes in food production and competitor density affect

feeding-territory area, energetic relationships, and time budgeting (Hixon, 1980). These models have been successful in predicting the territorial dynamics of migrant hummingbirds (Carpenter *et al.*, 1983; Hixon *et al.*, 1983). Applying such models to breeding animals should allow field workers to test the validity of this approach for studying the determinants of mating systems. A major conclusion of this analysis is that the predictions of the models are highly assumption dependent, so I include a thorough discussion of the assumptions and their consequences.

FORAGING, REPRODUCTION, AND TERRITORY AREA

Before developing the models mathematically, the predicted effect of natural selection upon feeding-territory area in breeding animals must first be examined. This requires a determination of the general foraging mode of females *versus* males at the onset of the breeding season when the mating system is established. Despite the empirical difficulties of such determinations (Hixon, 1982), some general expectations can be derived from basic principles. Schoener (1971) convincingly argued that the reproductive success of females should most often be limited by energy rather than by any other resource. He coined the term *energy maximizer* to describe the predicted female foraging behavior. Subsequently, modelers defined the optimum territory area for such foragers to be that which provided a maximum net energy gain in terms of the gross benefit derived from the food within the territory minus the cost of defending that territory (*e.g.*, Dill, 1978; Ebersole, 1980; Hixon, 1980; Schoener and Schoener, 1980; Schoener, 1983). Thus, in situations where females defend long-term individual feeding territories, it is reasonable to expect that selection will favor those individuals defending areas closest to the optimum for energy maximizers.

Schoener (1971) predicted further that, unlike females, a nongrowing male should forage as a *time minimizer*. Because the reproductive success of males is more often limited by access to females than by energy

(Bateman, 1948; Trivers, 1972), males should have relatively fixed energetic requirements. Further, a breeding male especially should obtain these requirements in a minimum amount of foraging time, thus freeing time for courtship and other activities immediately contributing to his reproductive success. Exactly how a territorial male should spend this extra time depends upon whether or not females are also territorial, and whether or not mate choice is operating.

Case I: In situations where only males are territorial and female choice of mates occurs, the basis of female choice becomes important. Females may select mates on the basis of three general criteria, either alone or in combination:

(1) *Females may base their choice solely upon some quality of the male himself, in which case male territory area is unimportant* (Weatherhead and Robertson, 1977a, b). If females choose males that spend the most time and effort in courtship activities independent of territorial behavior, then a male should defend a foraging area just large enough to provide his own energy requirements (Hixon, 1980). In some circumstances, this may ultimately lead to the evolution of leks, where the male's "territory" is simply a courtship display station and no longer a foraging area (Bradbury, 1981). This situation will not be further discussed in this paper.

(2) *The basis of female choice may be the abundance of some resource within the male's territory independent of territory area* (Brown and Orians, 1970). In this situation, the male defending the most resource may secure the most mates, resulting in "resource-defense polygyny" (Emlen and Oring, 1977). Hence, a male should invest his time in defending the largest area possible, thereby including as much of the resource as possible within his territory (Hixon, 1980). Males with the largest territories will not necessarily secure the most mates, since a small territory in a dense patch may contain more of the resource than a large territory in a sparse patch. However, the best that a male can do in a given patch is to defend the largest area possible.

(3) *The basis of female choice may simply be the area of the male's territory independent of resource density* (O'Donald, 1977). Here, a male should obviously defend the largest area possible, and males with the largest territories should secure the most mates.

Therefore, when the basis of female choice is either the abundance of some resource within the male's territory or simply the area of the territory itself, a male should still *forage* as a time minimizer, but should maximize the number of females he secures, and thus his potential reproductive success, by defending as an *area maximizer* (*sensu* Hixon, 1980). Thus, he should invest most of his "free" time in territorial activities rather than in courtship per se.

Case II: In situations where both sexes are independently territorial, female choice is not as important in determining mating systems as the pattern of spatial overlap among territories (Stamps, 1983). Here, the larger the male's territory, the greater the probability that his territory will include more than one female area, and thus that he will secure additional mates. Again, the male should forage as a time minimizer, but defend as an area maximizer (Hixon, 1980).

Thus, in modeling breeding situations where territory area is important, I will assume that males are "area maximizers" (Cases I and II) and that territorial females are "energy maximizers" (Case II only). In each case, I will derive expressions describing the determinants of territory area and other parameters relevant to reproductive success. I will then use these expressions to predict how differences (either between territories at the same time or between times within the same territory) in both food production and competitor density will affect territory area and time budgeting. Finally, I will use these predictions to determine concurrent changes in, first, the probability of a territorial individual mating polygynously, and second, the probability of that individual's reproductive success increasing. I will show that these two probabilities do not always covary. I will conclude each section with a review of the few data that are available to test these ideas and close with a brief discussion of approaches for further field tests. I encour-

age those empiricists who do not read the models to at least read the final section of this paper.

Assumptions

The following sets of major assumptions of the models will allow field workers to determine, *a priori*, the extent to which the generated predictions are relevant to their particular systems. Presenting these assumptions in detail is important because the predictions of territory-area models are notoriously assumption dependent (see also Schoener, 1983; McNair, 1987; Schoener, 1987). Subtle changes in assumptions can produce dramatic shifts in predictions, so matching each study system with the appropriate model is essential for meaningful field tests. As noted below, some assumptions are more important than others.

For easy reference, the symbols and units of the parameters used in the models are defined in Appendix I. Also listed in that appendix are some basic relationships between the parameters, which are self-explanatory and should be reviewed before proceeding beyond this section.

(1) *The system is deterministic and equilibrial.* Although simplistic, this assumption has been shown to be reasonable for systems that undergo considerable short-term fluctuations, such as hummingbird territories (Hixon *et al.*, 1983). Moreover, Lima (1984) has shown theoretically that a forager comparable to an energy maximizer, *i.e.*, an animal that is selected to minimize its probability of starvation in a stochastically variable environment, responds to changes in food production and competitor density in virtually the same ways as an energy maximizer in a deterministic system (Hixon, 1980; see also McNair, 1987). Adequate models of area maximizers in a stochastic system have not been developed. Ultimately, whether the environment varies deterministically or stochastically is not as important as whether the territory occupant can track that variability.

(2) *Each territory occurs within a patch that is homogeneous with respect to the distribution of food, other resources, and competitors.* This assumption greatly simplifies the mathe-

matics of the model, and violations do not strongly alter the predictions. Thus, at any given rate of food production (F), the daily availability of food within the territory, the time required to consume that food (T_r), and the energy potentially obtainable from that food (E_a) will all increase linearly with territory area (Fig. 1A). Therefore, should F increase, the slope of the E_a curve will increase. The slope of the T_r curve will also increase if F increases without a compensatory increase in the feeding efficiency (f). Despite the assumed homogeneity within patches, the overall habitat may be heterogeneous. Thus, the model allows for variations in territory quality, some patches containing more densely distributed resources than others.

(3) *In the case of energy maximizers, the total daily food production within the territory is consumed by the territory occupant*; food does not accumulate within the territory. As shown and discussed below, this may not be true for area maximizers, who will save a certain amount of food energy within the territory each day (E_s). This spare food will accumulate unless it is consumed by the territory occupant's mate(s).

(4) *The primary competitors in terms of the cost of territorial defense are nonterritorial individuals.* This assumption takes into account the fact that territorial neighbors often habituate to each other's presence after territory establishment (review by Hixon, 1980; see also Getty, 1987). I also assume that territorial defense effectively excludes all intruders, which will be true when the occupant can readily survey and quickly move about the entire territory (*e.g.*, small territories in open habitats). Finally, I assume that at any given competitor density (C), the temporal (T_c) and energetic (E_c) costs of defense increase linearly with territory area (Fig. 1A; see Hixon [1980] for details). Thus, should C increase, the slopes of the T_c and E_c curves will also increase. Schoener (1983) considers the effects of relaxing the assumption of linearity for territory-area models. In some cases, shifting from linearity to nonlinearity may alter the resulting predictions. However, linearity will be retained here for two reasons. First, virtually no data are available to determine whether linear or nonlinear functions are more common in nature. Second, available data do indicate that linearity adequately describes these functions in migrant hummingbirds (Carpenter *et al.*, unpublished), and linearity has proven to be a reasonable assumption for modeling territory area in these animals (Hixon *et al.*, 1983). In any case, because the predictions of the models may sometimes be changed by altering the shapes of the functions, it is important to determine empirically the relationship between defense costs (time or energy) and territory area for any study system. The linear models presented here can be reformulated to fit nonlinear situations using the same conceptual approach.

(5) *The time scale over which benefits and costs are measured is one day.* Obviously, this may be unrealistic for some systems (Davies and Houston, 1984). The model can be adjusted by redefining the parameters on a different temporal basis (*e.g.*, weekly rather than daily). Provided that temporal fluctuations in the parameter values are not too great, this adjustment eliminates problems associated with the future "prospective value" of the territory (*sensu* Stamps and Tollestrup, 1984), and does not affect the resulting predictions.

(6) *The models consider the period of the breeding cycle after territory establishment when mates are being chosen, before young are present and any parental care is required.* Thus, the individual's activity budget involves a fixed amount of time each day required for necessary courtship or self-maintenance activities independent of territory area. The remainder of the day (T_T) is spent either defending the territory (T_c) with its associated energetic cost (E_c), or feeding within the territory (T_f) with its associated energetic benefit (E_f), both of which vary with territory area as depicted in Figure 1A. With all environmental factors held constant, T_c (and thus E_c) must always increase with increasing territory area (A) for territoriality to persist; otherwise, the added area would be undefended. Therefore, beyond some critical area (A' in Fig. 1A), any further increase in A will result in a decrease in T_f (and thus E_f) as defense costs necessarily increase; only at or below A' can
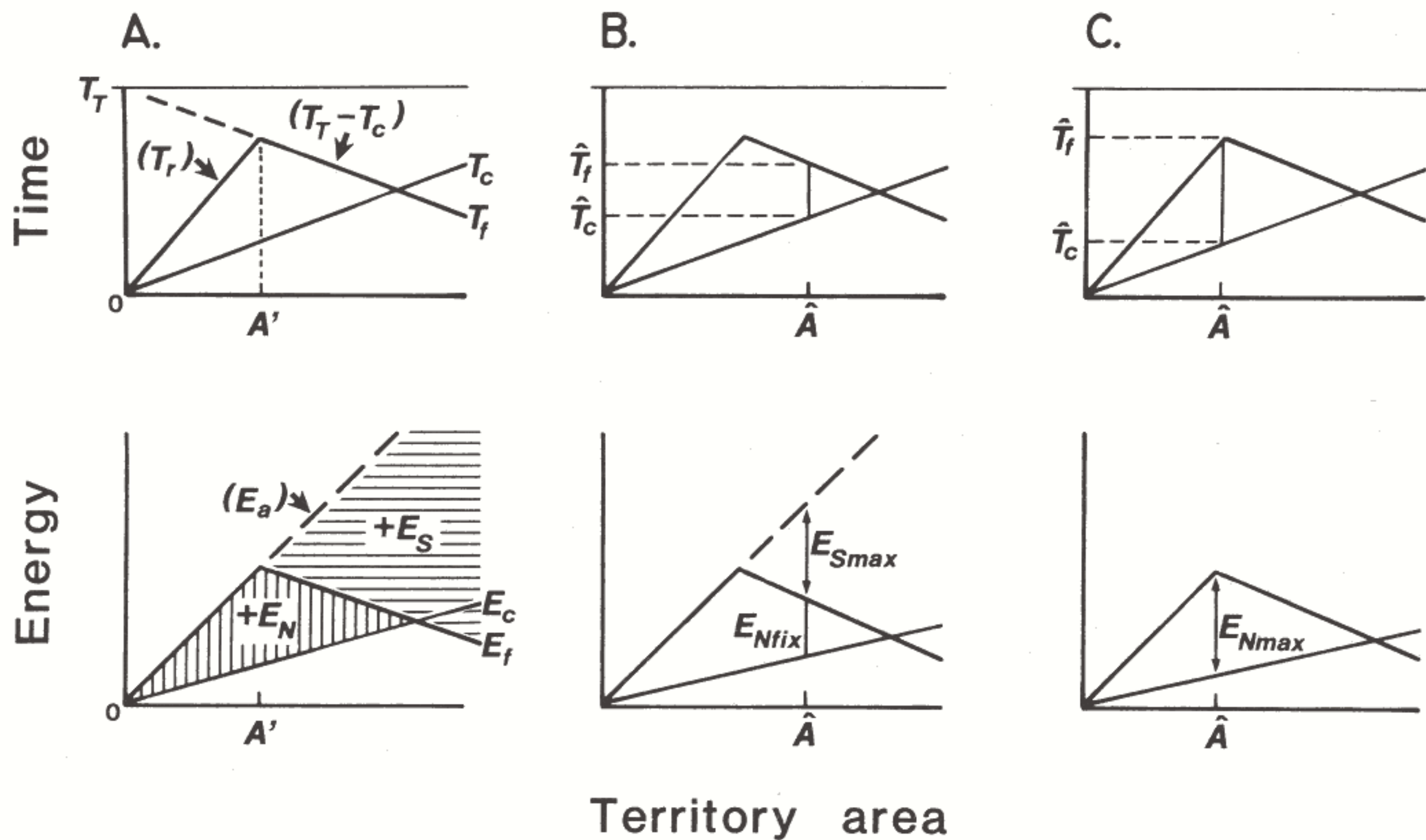
Territory area

FIG. 1. Structural framework of the models. A. Time relationships (top) illustrating the time constraint, such that below A' the T_f curve can equal T_r, while above A' the T_f curve becomes $(T_T - T_c)$. Energy relationships (bottom) illustrating the range of territory areas where E_N is positive. Because of the time constraint, the E_f curve equals E_a below A', but descends above A', resulting in the defense of spare food energy reserves (E_S). See Appendix I for definitions of symbols. B. The baseline system for a male area maximizer. The optimal territory area ($\hat{A}$) is the largest which supplies the fixed energy requirement (E_{Nfix}), thus maximizing E_S (i.e., E_{Smax}). C. The baseline system for a female energy maximizer. The optimal territory area ($\hat{A}$) is that which supplies the maximum net energy gain (E_{Nmax}). For both foragers the time budget at $\hat{A}$ is indicated for feeding ($\hat{T}_f$) and defense ($\hat{T}_c$).

$T_f = T_r$ and $E_f = E_a$ (Fig. 1A). In other words, there are only so many hours in the day, so beyond a certain territory area an increase in one activity (defense) will be at the expense of another (feeding). Thus, these models assume the existence of time constraints. (Schoener [1983] also considers "processing constraints," such as satiation, which will not be modeled here.) The net result is a finite range of territory areas where the daily net energy gain from territorial activities (E_N) is positive (Fig. 1A). Further, above some critical territory area (A'), the territory will contain spare food energy (E_S) available for potential mates (Fig. 1A).

(7) *The animal can expand and contract its territory in response to accurately perceived environmental changes.* If the territory either is contiguously surrounded by other territories (Hixon, 1980) or occupies a patch surrounded by unproductive or inhospit-

able habitat (the "hard edge" of Stamps *et al.*, 1987), then changes in territory area may be constrained by external factors beyond the occupant's control. In such cases, it may be worthwhile for the animal to establish a fixed territory of sufficient area to see it through the worst possible conditions (von Schantz, 1984). I also assume that changes in territory area are not strongly constrained by either travel time or risk of predation. This assumption may be violated in situations where either central-place territories are large (see Andersson, 1978) or predators are abundant (see Covich, 1976).

(8) *Competitor density in the vicinity of the territory may vary independently of food production* (e.g., Mares *et al.*, 1982, Mares and Lacher, 1987) *or increase with food production* (e.g., Myers *et al.*, 1979; Hixon *et al.*, 1983). I will model both situations separately, assuming a linear relationship when

competitor density increases with food production. Whether the curve describing the increase of competitor density with increasing food production is linear, accelerating, or decelerating can sometimes affect the resulting predictions. I will indicate these effects.

(9) *The feeding efficiency of the territory occupant (f), in terms of the biomass of food consumed per unit feeding time, may either be constant or increase with food density.* I will model both situations separately, assuming a linear relationship when feeding efficiency increases with food production. Again, the shape of the curve describing the relationship between food production and feeding efficiency can sometimes affect the resulting predictions. I will indicate these effects.

MODELS

Because of Assumptions (8) and (9) above, there are five possible environmental scenarios that must be modeled: (1) a change in food production (F) alone; (2) a change in F that concurrently affects feeding efficiency (f); (3) a change in F that concurrently affects both f and local competitor density (C); (4) a change in F that concurrently affects C but not f; and finally, (5) a change in C alone. Before considering each scenario, general expressions describing the optimal territory area ($\hat{A}$) for both sexes, the spare food energy defended by area-maximizing males (E_{Smax}), and the net energy gain of energy-maximizing females (E_{Nmax}) must first be derived.

The optimal (*i.e.*, largest possible) territory area for an area-maximizing male can be derived by manipulating the following basic relationships outlined in Appendix I:

$$E_{Nfix} = \hat{E}_f - \hat{E}_c = \hat{T}_f fy - \hat{T}_c d$$
$$= (T_T - C\hat{A}t)fy - C\hat{A}td$$

Solving for $\hat{A}$:

$$\hat{A} = \frac{T_T fy - E_{Nfix}}{Ct(fy + d)} \quad (1)$$

By definition, the amount of spare food energy saved within an area maximizer's territory each day is:

$$E_{Smax} = \hat{E}_a - \hat{E}_f = F\hat{A}y - \hat{T}_f fy$$
$$= F\hat{A}y - (T_T - C\hat{A}t)fy \quad (2)$$

The optimal (*i.e.*, E_N maximizing) territory area for an energy-maximizing female can be derived by similar manipulations of the relationships summarized in Appendix I:

$$T_T = \hat{T}_r + \hat{T}_c = F\hat{A}/f + C\hat{A}t$$

Solving for $\hat{A}$:

$$\hat{A} = \frac{T_T}{(F/f) + Ct} \quad (3)$$

Because $E_f = E_a$ for an energy maximizer, the daily net energy gain of this forager is:

$$E_{Nmax} = \hat{E}_a - \hat{E}_c = F\hat{A}y - C\hat{A}td \quad (4)$$

These key variables (equations 1–4) are illustrated graphically in Figure 1B for a male area maximizer and Figure 1C for a female energy maximizer. To determine how these variables change with each of the above five scenarios one must, first, incorporate the expressions $f = k_1 F$ and $C = k_2 F$ into equations (1–4), and second, calculate the derivative of each expression with respect to the given independent variable. This procedure is summarized in Appendix II. If the sign of the first derivative is positive, the dependent variable increases as the independent variable increases, and vice versa. If the first derivative is zero, the "dependent variable" is constant with respect to changes in the independent variable. Thus analyzed, the predicted changes of $\hat{A}$, E_{Smax}, and E_{Nmax} in each of the five scenarios are listed in Table 1 (discussed below). Improving on my original graphs (Hixon, 1980), Schoener (1983) has illustrated the dynamics of these predictions for energy maximizers in Scenario (1) (his Fig. 2), Scenario (4) (his Fig. 7), and Scenario (5) (his Fig. 4).

To determine predicted changes in the time budgets (daily feeding time [$\hat{T}_f$] and defense time [$\hat{T}_c$]) of males and females in each of the five scenarios, a similar anal-

ysis is used. The major expressions are that $\hat{T}_c = CAt$ for both sexes, that $\hat{T}_f = \hat{T}_r = FA/f$ for females only, and that due to the time constraint $\hat{T}_f = T_T - \hat{T}_c$ for both sexes. Thus analyzed, the predicted changes in the time budgets of both sexes in each of the five scenarios are also listed in Table 1. I will now consider these predictions in terms of the resulting mating system and reproductive success of individuals in the two kinds of territorial systems.

CASE I: ONLY MALES TERRITORIAL

Examples

This situation appears to be common in birds (review by Wittenberger, 1981). Typically, males arrive at the breeding grounds first and establish individual territories. Arriving females then distribute themselves among the males' territories, presumably basing their choices upon the relative qualities of the territories. The classic Verner-Willson-Orians model illustrates how relatively large differences in territory quality will select for females mating polygynously with the occupant of a high-quality territory rather than monogamously with the occupant of a low-quality territory (Verner, 1964; Verner and Willson, 1966; Orians, 1969). Recent reviews indicate that such resource-defense polygyny also occurs in insects (Thornhill and Alcock, 1983) and possibly anuran amphibians (Wells, 1977; Arak, 1983). Isolated cases may also be found in fishes inhabiting coral reefs (Fricke, 1980; Schmale, 1981), temperate reefs (Jones, 1981; Cole, 1984), and freshwater habitats (Assem, 1967; Constanz, 1975), as well as in some lizards (Schoener and Schoener, 1980, 1982) and large mammals (Jarman, 1974). In nonavian vertebrates, the males are often territorial year-round.

As argued above, when females in Case I base their choice of mates upon male territory quality, the parameters determining a male's reproductive success will be territory area (A) and/or the food reserves included within the territory (E_S). The greater the value of A and/or E_S an individual male can maintain relative to all other males in the system, the greater is the probability of that male becoming polygynous. Ultimately, the exact probability depends upon a variety of factors acting in concert with male territory quality (Vehrencamp and Bradbury, 1984), including the operational sex ratio (Emlen and Oring, 1977). Because such factors may be beyond the control of an individual male, his best option is to maximize A and E_S by being an area maximizer in the most resource-rich microhabitat he can defend (Fig. 1B).

Studies of birds provide four lines of circumstantial evidence that males in Case I behave (or should behave) as area maximizers. First, male mating success often increases with territory quality (reviews by Orians, 1980; Searcy and Yasukawa, 1983), which may include the abundance of food on the territory (e.g., Verner, 1964; Wittenberger, 1980) or the abundance of other resources such as shelter (e.g., Pleszczynska, 1978; Searcy, 1979). For example, by experimentally increasing the abundance of sheltered nest sites on male territories, Plesczynska and Hansell (1980) increased the incidence of polygyny in lark buntings (Calamospiza melanocorys). At any given density of sheltered nest sites, males with larger territories would increase their probability of securing more than one mate. Second, clutch size is known to increase with the abundance of food on the territory (e.g., Hogstedt, 1980; van Riper, 1984), which may select for area maximization in habitats where food supplies increase with territory area. Indeed, field experiments have shown that males defend more than minimal food requirements (e.g., Wasserman, 1983). Third, in some systems females select the largest male territories, either because territory area may reflect the abundance of resources within (e.g., Yasukawa, 1981) or simply because territory area itself may be a sexually selected trait (e.g., O'Donald, 1977; Price, 1984). Fourth, in hummingbirds that are territorial year-round, males expand their territories at the beginning of the breeding season, increasing their allocation of time to defense (e.g., Stiles, 1971), which is consis-

TABLE 1. *Predicted responses[a] of territory parameters of males and females following increases in food production (F), feeding efficiency (f), and / or competitor density (C) for five different scenarios.[b] Predictions would reverse following decreases in the same factors. See Appendix I for definitions of symbols.*

	Increased variable			Predicted response							
				Male area maximizer				Female energy maximizer			
Scenario	F	f	C	(1) A	(2) E_{Smax}	(3) $\hat{T}_f$	(4) $\hat{T}_c$	(5) A	(6) E_{Nmax}	(7) $\hat{T}_f$	(8) $\hat{T}_c$
(1)	X			nc	↑	nc	nc	↓	↑	↑	↓
(2)	X	X		↑	↑	↓	↑	nc^c	↑	nc^d	nc^c
(3)	X	X	X	↑ or ↓^e	↑ or ↓^f	↓	↑	↓	↑ or ↓^f	↓	↑
(4)	X		X	↓	nc^g	nc	nc	↓	nc^g	nc^g	nc^h
(5)			X	↓	↓	nc	nc	↓	↓	↓	↑

[a] ↑ = increase; ↓ = decrease; nc = no change.

[b] Predictions for Scenarios 2–4 assume f and/or C increase linearly with F. Nonlinearity does not change predictions except as indicated below.

[c] If increase in f is concave upward, then parameter increases, and vice versa.

[d] If increase in f is concave upward, then parameter decreases, and vice versa.

[e] See Appendix II (footnote b) and Figure 2 for conditions.

[f] See Appendix II (footnote c) for conditions.

[g] If increase in C is concave upward, then parameter decreases, and vice versa.

[h] If increase in C is concave upward, then parameter increases, and vice versa.

tent with area maximization. Note, however, that female territoriality in birds may be more common than previously supposed (Hurly and Robertson, 1984, 1985), so many putative Case I systems may actually belong to Case II.

In nonavian vertebrates, evidence for male area maximization is more tenuous. For example, males of some fish species expand their permanent territories at the onset of the breeding season (Moran and Sale, 1977; Cole, 1984). This behavior may indicate a shift to an area-maximizing mode, or simply reflect a seasonal environmental change. In other fishes, males with larger territories secure more mates (Assem, 1967; Constanz, 1975; Fricke, 1980). This pattern may indicate selection for area maximization, or again, may be a mere correlation. Moreover, there are exceptions to this pattern (Jones, 1981; Schmale, 1981; Cole, 1982). Stamps and Buechner (1985) have recently reviewed the evidence for area maximization in terrestrial vertebrates.

Predictions

Male territory area. Suppose that the basis of female choice is male territory area per se or some evenly distributed non-food resource. In such circumstances, the probability of a given male mating polygynously (P[polygyny]) varies directly with the area

of his territory (A). Examining column (1) of Table 1, if food production (F) within a single territory increases, then $\hat{A}$ and thus P[polygyny] will remain unchanged (Scenario 1), increase (Scenario 2), or decrease (Scenario 4), depending upon the relationships between F, the feeding efficiency (f), and local competitor density (C). In Scenario (3), $\hat{A}$ will either increase or decrease, depending upon the conditions described in Figure 2. The bottom line is that predicting changes in P[polygyny] following changes in F requires considerable knowledge of the system. If, on the other hand, C increases in the vicinity of a single territory, then $\hat{A}$ and thus P[polygyny] will usually decrease (Table 1, column 1, Scenarios 3–5).

Male territory food reserves. Suppose, however, that the basis of female choice is the abundance of food reserves within the territory (E_S) rather than either territory area per se or some direct correlate of area. In this situation, P[polygyny] varies directly with E_{Smax}. Thus, examining column (2) of Table 1, if F within a single territory increases, then E_{Smax} and thus P[polygyny] will increase as long as C does not increase concurrently (Scenarios 1 and 2). Otherwise, the outcome depends upon the particularities of the system (Scenarios 3 and 4). If C in the vicinity of a single territory increases, then predicting changes in E_{Smax}

and thus P[polygyny] requires detailed knowledge of the system (Table 1, column 2, Scenarios 3–5).

Generalities. Besides illustrating the strong assumption-dependence of the models, these analyses predict some fundamental differences between systems where the basis of female choice is, on one hand, territory area per se or some direct correlate of area, and on the other hand, the abundance of food reserves within the territory. First, where females choose territory area, the predictability of changes in the probability of individual males becoming polygynous is greater when considering the effects of competitor density; food-production effects are less predictable without knowledge of the relationships between food production, feeding efficiency, and competitor density. Conversely, where females choose food reserves, predictability is greater when considering the effects of food production; competitor-density effects are less predictable.

Second, and more important, changes in local food production can have different (indeed, opposite) effects upon an individual male's probability of becoming polygynous, depending upon the basis of female choice. In Scenario (1) an increase in food production will not affect male territory area, yet increase his food reserves, while in Scenario (4) an increase in food production will cause a decrease in territory area, yet not affect the food reserves (Table 1, columns 1 and 2). In the most complex situation (Scenario 3) where both feeding efficiency and competitor density are linear functions of food density, predicting the effects of an increase in food production requires knowledge of additional parameter values. Whether male territory area increases or decreases depends upon whether or not the quantity $E_f + E_{Nfix}$ is greater than the quantity $T_T k_1 F y$ (Fig. 2). Whether food reserves increase or decrease depends upon whether or not the parameter y is greater than the quantity $k_2 t d$ (Appendix II). Because these four quantities can vary independently of each other, it is possible to have an outcome where an increase in food production increases male territory area yet decreases his food reserves (or vice versa), thus having oppo-
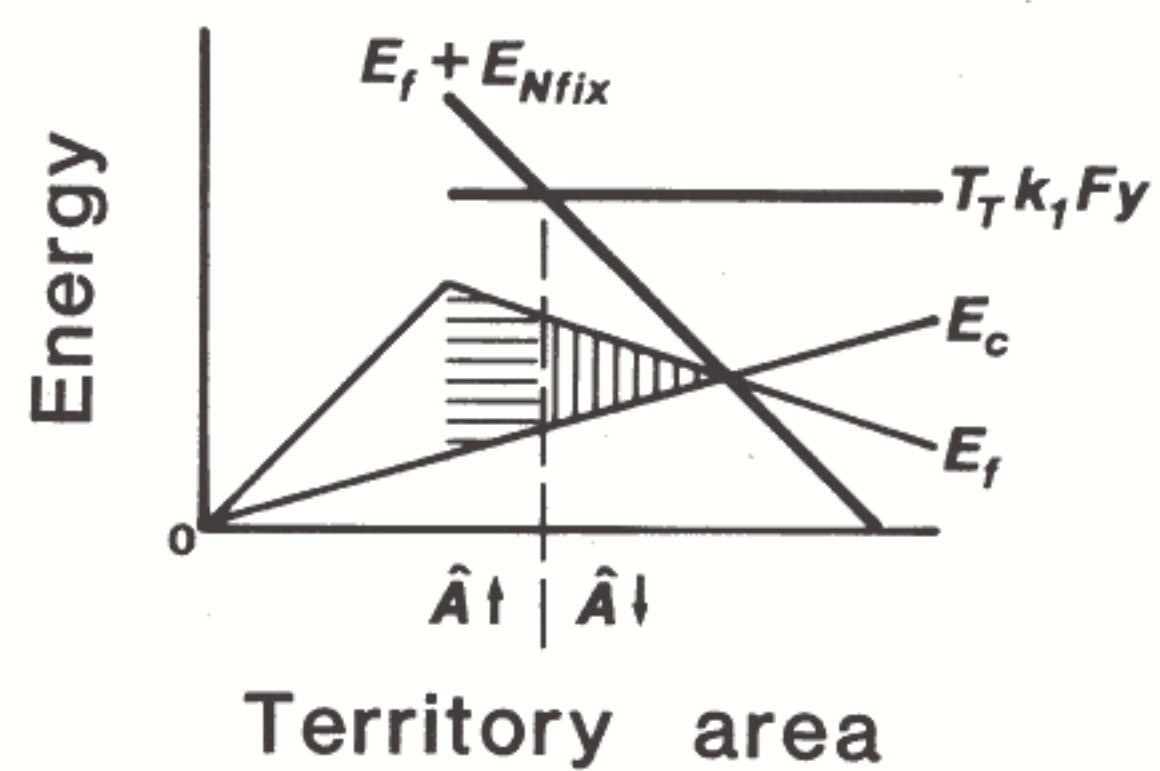

FIG. 2. Conditions under which the territory area of an area maximizer will increase or decrease following an increase in food production (F) in Scenario 3 (Table 1). The figure is identical to Fig. 1B, with two additional curves depicting $T_T k_1 F y$ (quantity 1, which varies independently of A) and $E_f + E_{Nfix}$ (quantity 2, which varies inversely with A). The hatched regions include all possible positive values of E_{Nfix} for an area maximizer. From the derivative of the expression for $\hat{A}$ in Appendix II, if E_{Nfix} is sufficiently large (horizontally hatched region), then $\hat{A}$ will increase as F increases because quantity 1 is less than quantity 2 (left side of dashed vertical line). Otherwise (vertically hatched region), $\hat{A}$ will decrease (right side of dashed vertical line).

site effects on his potential reproductive success, depending upon the basis of female choice.

Evaluation

Few data are available to test the predictions in Table 1 (columns 1–4), since few researchers have included analyses of male territory area, food reserves, time budgets, and mating success in a single study. Perhaps the most relevant experimental study of a Case I system is that of Ewald and Rohwer (1982), who placed feeders in the territories of red-winged blackbirds (*Agelaius phoeniceus*). When a single feeder was added, male territory area did not change, but the number of nesting females increased relative to control territories. When the density of feeders was increased by approximately an order of magnitude, male territory area decreased and the number of nesting females did not change significantly.

These data are consistent with the predictions for a system where feeding efficiency is constant. In the first experiment, food production increased without a concurrent increase in local competitor density as measured by intrusion rates; non-territorial males apparently did not detect

the single feeder. As predicted for this situation (Scenario 1 in Table 1), male territory area did not change, food reserves (E_{Smax}, the presumed basis of female choice) increased, and consequently, so did the extent of polygyny (from an average of 3.4 to 4.7 females per male territory). Moreover, the time budgets of the experimental males did not change appreciably (Ewald, personal communication), also as predicted. In the second experiment, an increase in food production was accompanied by an increase in local competitor density; average intrusion rates increased nearly fivefold. As predicted for this situation (Scenario 4 in Table 1), territory area decreased and the extent of polygyny (presumably correlated with E_{Smax}) did not change.

However, there are potential problems with this interpretation. First, changes in overall food reserves within the territories as well as detailed male time budgets were not reported. Therefore, the evidence supporting the predictions for Scenarios (1) and (4) is both circumstantial and incomplete. Second, feeding efficiencies were not measured. If feeding efficiencies did increase, which is possible given that feeders are predictable and easily exploited food sources, then Scenarios (2) and (3), rather than (1) and (4), become relevant. In the first experiment (now Scenario 2 in Table 1), the prediction that territory area should have increased is falsified, while the prediction that food reserves and thus the extent of polygyny should have increased is supported. However, territory expansion apparently was prevented by contiguously territorial neighbors (Ewald, personal communication), so Assumption (7) was violated in this system. In the second experiment (now Scenario 3 in Table 1), insufficient information about the system was reported to predict changes in territory area or food reserves (see Appendix II, footnotes b and c). In any case, recent observations and experiments have suggested that females as well as males may be territorial in other red-winged blackbird systems (Hurly and Robertson, 1984, 1985), which are thus better included with Case II systems.

CASE II: BOTH SEXES TERRITORIAL

Examples

This situation is common in many lizards (review by Stamps, 1983). Typically, both sexes defend feeding territories, with male areas overlapping those of females, but with little male-male or female-female overlap. Similar systems may occur among some coral-reef fishes (e.g., Robertson and Hoffman, 1977; Hoffman, 1983), some birds (e.g., Davies and Lundberg, 1984; Hurly and Robertson, 1984), and some mammals (reviews by Macdonald, 1983; Stamps and Buechner, 1985).

Evidence that males in Case II systems behave as area maximizers is circumstantial. Stamps (1983) and Stamps and Buechner (1985) review numerous cases of territory expansion by male lizards and rodents occurring at the onset of the breeding season, perhaps indicating a shift from a time-minimizing to an area-maximizing mode. The existence of this shift has been corroborated by a study which verified the predictions that (1) the territory of a nonbreeding time minimizer should always contract following an increase in only food production (Hixon, 1980), while (2) that of a breeding area maximizer should not (Table 1, column 1, Scenarios 1 and 2). Simon (1973, 1975) found that adding food to territories of male lizards (*Sceloporus jarrovi*) resulted in territory contraction during the nonbreeding season, but not during the breeding season. Additionally, breeding males defend territories much larger than required to fulfill their food requirements and males with larger territories secure more mates in some lizards (Schoener and Schoener, 1982; Stamps, 1983), birds (Davies and Lundberg, 1984; Harper, 1985), and small mammals (review by Stamps and Buechner, 1985).

As argued above, territorial females should behave as energy maximizers, and thus defend areas providing the maximum net energy gain (Fig. 1C). Evidence that females in Case II systems behave as energy maximizers has been provided only for protogynous reef fishes. Hoffman (1983) demonstrated experimentally that when

female wrasses (*Bodianus* spp.) change sex, the amount of time they spend feeding declines as they devote more time to aggressive behaviors. This outcome corroborates a prediction from the structural framework of the model that male area maximizers should spend less time feeding and more time defending their territories (Fig. 1B) than female energy maximizers in the same system (Fig. 1C).

Predictions

Because both males and females are independently territorial, the mating system in Case II becomes a function of how many female territories are included within each male territory (Stamps, 1983). Thus, where male and female territories overlap, the probability of polygyny occurring increases as male (area-maximizer) territory area increases and/or female (energy-maximizer) territory area decreases. In attempting to model this situation, two important questions must be addressed. First, do the two sexes eat the same food? If so, assuming that males are dominant and consume what they need first, then the spare food reserves within their territories (E_{Smax}) become the food supplies available to the territorial females (E_a), so that the equations determining territory area in males and females become linked. Space limitations do not allow me to consider this interesting (albeit complex) situation here. However, if the sexes eat the same food but partition that food in some way, or if the sexes eat different foods as a result of sexual dimorphism (*e.g.*, Selander, 1972; Schoener, 1977), then male and female food supplies may be considered independently. I will assume this to be the case, and provide predictions only for situations in which food productions for territorial males and females vary in the same direction (*i.e.*, food production either increases or decreases for both sexes concurrently).

Second, who are the territory intruders for the two sexes? Territorial males should obviously exclude unrelated nonterritorial males, but may or may not exclude nonterritorial females, depending upon their ability to secure those females as mates. Territorial females should obviously

TABLE 2. *Predicted changes*[a] *in the probabilities of polygyny occurring (column 1) and of female (column 2) and male (column 3) reproductive success increasing following increases in food production (F), feeding efficiency (f), and / or competitor density (C) for five different scenarios in systems where both sexes are territorial (Case II).*

	Increased variable				P[RS]	
Scenario	F	f	C	(1) P[polygyny][b]	(2) Female[c]	(3) Male[d]
(1)	X			↑	↑	↑
(2)	X	X		↑	↑	↑
(3)	X	X	X	↑ or ↓[e]	↑ or ↓[e]	↑ or ↓
(4)	X		X	↓	nc	↓
(5)			X	↓	↓	↓

[a] ↑ = increase; ↓ = decrease; nc = no change.
[b] Varies with male $\hat{A}$/female $\hat{A}$ (see Table 1).
[c] Varies with E_{Nmax} (see Table 1).
[d] Varies with both P[polygyny] and female P[RS].
[e] See Table 1 and text for conditions.

exclude unrelated nonterritorial females, but may or may not exclude nonterritorial males, depending upon intersexual dominance relations. Rather than treating a number of specific cases, I will provide predictions only for situations in which competitor densities for territorial males and females covary, regardless of who those competitors are.

Probability of polygyny. Given the assumptions and conditions discussed above, and that the probability of polygyny occurring (P[polygyny]) varies directly with the ratio of male territory area to female territory area, column (1) of Table 2 lists the predicted effects of changes in F and C upon P[polygyny]. The ratio of territory areas is calculated by combining the respective individual predictions for male and female territory areas from Table 1 (columns 1 and 5). For example, if only food production (F) increases for both sexes (Scenario 1), then male territory area will not change (Table 1, column 1) and female territory area will decrease (Table 1, column 5). Therefore, the ratio of territory areas and thus P[polygyny] will increase (Table 2, column 1, Scenario 1). Similarly, if F increases with a concurrent increase in feeding efficiency (Scenario 2), then male territory area will increase (Table 1, column 1) and female territory area will not change (Table 1, column 5). Therefore, the ratio of territory areas and thus

P[polygyny] will again increase (Table 2, column 1, Scenario 2).

In situations where male and female territory areas both contract in response to the same environmental changes (Scenarios 3–5), it is necessary to know the relative rates of change of male and female areas by taking the ratio of their derivatives. In Scenarios (4) and (5), male territory area will always contract more rapidly than female territory area, so the ratio of territory areas will decrease (Table 2, column 1). This effect is illustrated for Scenario (5) in Figure 3 of Hixon (1980). Scenario (3) is more complex. Male territory area can either expand or contract, but when contracting it should do so more rapidly than female territory area, unless local competitor density increases very little. However, female territory area should always decrease. The bottom line is that predicting changes in the ratio of territory areas in this situation requires detailed knowledge of the system.

Thus, there are two basic predictions regarding P[polygyny] (Table 2, column 1): (1) If food production increases without a concurrent increase in local competitor density (Scenarios 1 and 2), then the ratio of male to female territory areas and thus the probability of polygyny will increase. (2) If competitor density increases without a concurrent increase in feeding efficiency (Scenarios 4 and 5), then the ratio of male to female territory areas and thus the probability of polygyny will decrease.

Female reproductive success. Female reproductive success is limited by net energy gain (E_{Nmax}). Therefore, transcribing column (6) of Table 1 to column (2) of Table 2 gives the predicted effects of changes in F and C upon the probability of a female's reproductive success increasing (P[RS]). Thus, if F increases without a concurrent increase in C (Scenarios 1 and 2), then P[RS] will increase. If, on the other hand, C increases with or without F (Scenarios 3–5), then any outcome is possible, depending upon the exact relationships between C, F, and f.

Male reproductive success. In Case II systems, a male's reproductive success is the product of the number of mates he secures and the average reproductive success of those mates. Therefore, predicting changes

in the probability that a male's reproductive success will increase (male P[RS]) requires knowledge of both his probability of becoming polygynous (P[polygyny]) and the probability that the reproductive success of his mate(s) will increase (female P[RS]). Thus, male P[RS] will be a combined function of the ratio of male territory area to female territory area (Table 2, column 1) and the net energy gain of each female (Table 2, column 2). Column (3) of Table 2 lists the resulting predicted effects of changes in F and C upon male P[RS]. The predictions parallel those for P[polygyny] (Table 2, column 1).

Note that, because of the variable outcomes in Scenario (3), it is possible that P[polygyny] and P[RS] may not covary. Therefore, inferring an increase in male reproductive success from an increase in the number of mates attained is not justified without knowing the reproductive success of those mates.

Evaluation

As for Case I, perhaps the most relevant experimental study of a Case II system deals with birds. Davies and Lundberg (1984, 1985) placed feeders in the territories of female dunnock (or hedge sparrow, *Prunella modularis*). In their system, both sexes were territorial and male territories overlapped those of females. Moreover, it was clear that adding food increased both feeding efficiency and local competitor density for both sexes, so that the manipulation produced Scenario (3). Table 3 compares the results of this experiment with the predictions for this scenario for nine different parameters. The model accurately predicted the responses of five parameters outright, with the responses of two others (the extent of polygyny and male reproductive success) being accurately predicted given partial information from the study. The response of another parameter (female reproductive success) was not predictable without additional, unreported information. The response of the remaining parameter (male territory area) was not accurately predicted by the model, since the actual outcome (no change) is the boundary outcome between the predicted increase or decrease with a near-zero prob-

Table 3. *Results of a food-enhancement experiment (Davies and Lundberg, 1984, 1985), in a system where both sexes were territorial (Case II) and both feeding efficiency and local competitor density increased concurrently (Scenario 3), compared with model predictions (see Tables 1 and 2). See Appendix I for definitions of symbols.*

	Extent of polygyny	Males				Females			
		A	T_f	T_c	RS	A	T_f	T_c	RS
Observed:	↑	nc	↓	↑	↑	↓	↓	↑	nc
Predicted:	↑[a]	↑ or ↓	↓	↑	↑[b]	↓	↓	↑	—[c]

[a] Given that male A did not change.
[b] Given that female RS did not change.
[c] Prediction not possible without additional information, given in Appendix II (footnote c).

ability of occurrence. Given that the model performed reasonably well for most parameters, it appears that Assumption (7), *i.e.*, no external constraints on changing territory area, may have been violated for males in this system. In fact, changes in male territory area were apparently prevented by contiguously territorial neighbors (Davies, personal communication). In any case, the success of the model is tentative, since many of the assumptions were untested for this system.

Tests, Limitations, and Caveats

From the field evidence reviewed in this paper, it is obvious that theory greatly exceeds field evidence concerning the determinants of territory area, especially considering the influence of territory area on mating systems. After working through the arrays of assumptions, scenarios, conditions, equations, and predictions presented in this paper and Schoener's (1983, 1987) reviews, a reasonable reaction would be: Why bother? A major rationale is that these analyses demonstrate the extreme assumption dependence of predictions from territory-area theory. The models can produce virtually any combination of predictions, depending entirely upon the details of the underlying assumptions. Such assumption sensitivity does not render the models worthless for field workers. On the contrary, these analyses show that accurately assessing the mechanisms by which environmental factors affect territory area, and thus mating systems, requires that the assumptions of the models be evaluated. This can be accomplished directly, by testing the assumptions as hypotheses in their own right, or indirectly, by testing multiple secondary predictions of the models.

Directly testing assumptions requires the modeler to list his or her assumptions explicitly and the field worker to determine whether those assumptions fit his or her system *before* undertaking a test of the predictions. This has rarely been accomplished. For example, Ebersole (1980) produced an intriguing model which predicted only that territory area should increase with increasing food density. He then performed uncontrolled additions of algae in and about the territories of the herbivorous damselfish *Eupomacentrus leucostictus*, and interpreted his results as demonstrating the validity of his model. Setting aside questions of data interpretation (see Norman and Jones, 1984), the problem is that Ebersole did not evaluate the assumptions of his model for the damselfish system, so accepting his model to the exclusion of others was not justified. In fact, Schoener (1983) showed that the prediction of territory area increasing with increasing food density can be generated by at least five different models, and Table 1 in this paper shows that three additional models can produce the same outcome. Which, if any, is appropriate for the damselfish system? There is no way of knowing unless the mechanisms underlying the observed results are compared with the assumptions underlying the models.

Table 4 lists some of the factors influencing territory area, about which implicit or explicit assumptions are made by all models, but which are commonly overlooked by researchers "testing" those models. In many systems, testing these assumptions directly may be difficult or even impossible. This should not discourage experimental analyses of such systems, but should discourage calling these analy-

TABLE 4. *Some commonly overlooked factors which must be considered for an adequate test of any model of feeding-territory area.*

External constraints:
    Contiguous territories
    Distribution and behavior of nonterritorial competitors
    Distribution and behavior of predators
    Distribution and quality of undefended food sources
    Habitat boundaries and discontinuities

Internal constraints:
    Time and energy limitations
    Food detection and processing
    Competitor detection and defense efficiency

Relationships:
    Between food production and feeding efficiency
    Between food production and competitor density
    Between territory area and food benefits
    Between territory area and defense costs

ses "tests" of particular models. Clearly, observing only the response of territory area to some manipulation tests no model completely.

Indirectly testing assumptions requires the modeler to generate as many secondary predictions as possible beyond those dealing with territory area. These secondary predictions, such as those involving time budgets, food reserves, and net energy gains, not only reflect the underlying mechanisms of a model, but also produce unique sets of predictions for any given set of assumptions. This is especially important for qualitative predictions of changes in territory area, since an area can only expand, contract, or remain unchanged following any given environmental change. Because only three outcomes are possible, the chance of a model making the right prediction for the wrong reason is high. Table 1 illustrates the importance of multiple predictions. For example, if one considers only changes in territory area, column (5) shows that nearly every scenario causes a decrease in this parameter for an energy maximizer. However, including predictions for time budgeting and net energy gain (columns 6–8) separates the outcomes of these scenarios.

Few field tests of territory-area models have included time-budget analyses, and all

these have been conducted during the non-breeding season. Hixon et al. (1983) provided evidence that migrant rufous hummingbirds (*Selasphorus rufus*) adjust the area of their territories according to the energy-maximizer model for Scenario (3) in Table 1. Subsequent studies have independently tested and verified their major assumptions (Carpenter et al., 1983; Diamond et al. 1986; Karasov et al., 1986). In a similar study, Norman and Jones (1984) provided evidence that the damselfish *Parma victoriae* behaves as an area maximizer according to Scenarios (1) and (5) in Table 1, although they did not discuss their data in these terms. Although time-budget analyses have proven valuable in these experimental analyses, there can be problems of interpretation. In particular, categorizing behaviors as either foraging or defense is not always straightforward (Hixon, 1982; Paton and Carpenter 1984). Thus, direct assessment of assumptions remains the best approach for evaluating the general validity of a model.

Ultimately, most analytical models subjected to detailed evaluation in the field are doomed to failure simply because models are simplified abstractions of our perceptions of reality. Yet, such analyses are valuable in that they suggest which factors might be important in determining territory area, and by extension, mating systems. All practical questions of testability aside, if these models do nothing more than encourage researchers to examine more closely the mechanisms that determine the areas of real territories and the structures of real mating systems, then these exercises will have been worthwhile.

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Appendix I

Symbol Definitions and Units

Basic variables:

A = territory area, m².

C = competitor density = daily intrusion rate of nonterritorial competitors per unit defended area, no. competitors/m².

F = food production = daily available food biomass produced per unit defended area, g/m².

f = feeding efficiency = food biomass consumed per unit feeding time, g/sec.

$P[\text{polygyny}]$ = probability of a territorial male securing more than one mate.

$P[\text{RS}]$ = probability of reproductive success increasing.

Energy variables (unit: J):

E_N = daily net energy gain from territorial activities ($=E_f - E_c$); value is fixed for males (E_{Nfix}) and maximized by females (E_{Nmax}).

E_S = daily spare food energy available for mate(s) within territory ($=E_a - E_f$); value is maximized by males (E_{Smax}).

E_a = daily available food energy produced within territory ($=FAy$).

E_c = daily total energy loss due to territory defense ($=T_c d$).

E_f = daily gross energy gain from territory food supplies ($=T_f f y$).

Time variables (unit: sec):

T_T = total daily time available for feeding and territory defense after any necessary courtship or self-maintenance activities ($\geq T_f + T_c$).

T_c = total daily time required for territory defense ($=CAt$).

T_f = total daily time spent feeding ($=T_T - T_c$ for both area maximizing males and energy maximizing females; $<T_r$ for area maximizers; $=T_r$ for energy maximizers).

T_r = total time required to consume daily food production within territory ($=(FA)/f$).

Variable modifier:

$\hat{v}$ = value of variable v at the optimal territory size.

Constants:

d = defense efficiency constant converting T_c to E_c, J/sec.

k_1 = food detection efficiency constant converting F to f, m²/sec.

k_2 = competitor attraction constant converting F to C, no. competitors/g.

t = temporal defense cost constant converting (CA) to T_c, sec/competitor.

y = energetic yield constant converting food biomass to available energy, J/g.

Appendix II
Mathematical Summary of Models

Scenario: Independent variable	Dependent variable	Derivative	Sign
MALE AREA MAXIMIZER:			
1: F with f and C constant:	$\hat{A} = \dfrac{T_T f_y - E_{Nfix}}{Ct(fy + d)}$	$\dfrac{d\hat{A}}{dF} = 0$	0
	$E_{Smax} = F\hat{A}y - (T_T - C\hat{A}t)fy$	$\dfrac{dE_{Smax}}{dF} = \hat{A}y$	+
2: F with $f = k_1 F$ and C constant:	$\hat{A} = \dfrac{T_T k_1 Fy - E_{Nfix}}{Ct(k_1 Fy + d)}$	$\dfrac{d\hat{A}}{dF} = \dfrac{T_f k_1 y}{Ct(k_1 Fy + d)}$	+
	$E_{Smax} = F\hat{A}y - (T_T - C\hat{A}t)k_1 Fy$	$\dfrac{dE_{Smax}}{dF} = \dfrac{T_c(y(k_1 Fy + d)) + T_f(k_1 y(Fy - Ctd))}{Ct(k_1 Fy + d)}$	+[a]
3: F with $f = k_1 F$ and $C = k_2 F$:	$\hat{A} = \dfrac{T_T k_1 Fy - E_{Nfix}}{k_2 Ft(k_1 Fy + d)}$	$\dfrac{d\hat{A}}{dF} = \dfrac{E_f + E_{Nfix} - T_T k_1 Fy}{k_2 F^2 t(k_1 Fy + d)}$	+ or −[b]
	$E_{Smax} = F\hat{A}y - (T_T - k_2 F\hat{A}t)k_1 Fy$	$\dfrac{dE_{Smax}}{dF} = \dfrac{E_f(y - k_2 td)}{k_2 Ft(k_1 Fy + d)}$	+ or −[c]
4: F with $C = k_2 F$ and f constant:	$\hat{A} = \dfrac{T_T fy - E_{Nfix}}{k_2 Ft(fy + d)}$	$\dfrac{d\hat{A}}{dF} = \dfrac{E_{Nfix} - T_T fy}{k_2 F^2 t(fy + d)}$	−
	$E_{Smax} = F\hat{A}y - (T_T - k_2 F\hat{A}t)fy$	$\dfrac{dE_{Smax}}{dF} = 0$	0
5: C with F and f constant:	$\hat{A} = \dfrac{T_T fy - E_{Nfix}}{Ct(fy + d)}$	$\dfrac{d\hat{A}}{dC} = \dfrac{E_{Nfix} - T_T fy}{C^2 t(fy + d)}$	−[d]
	$E_{Smax} = F\hat{A}y - (T_T - C\hat{A}t)fy$	$\dfrac{dE_{Smax}}{dC} = \dfrac{-FT_c y}{C^2 t}$	−
FEMALE ENERGY MAXIMIZER:			
1: F with f and C constant:	$\hat{A} = \dfrac{T_T}{(F/f) + Ct}$	$\dfrac{d\hat{A}}{dF} = \dfrac{-T_T}{f((F/f) + Ct)^2}$	−
	$E_{Nmax} = F\hat{A}y - C\hat{A}td$	$\dfrac{dE_{Nmax}}{dF} = \dfrac{T_T Ct(fy + d)}{f((F/f) + Ct)^2}$	+
2: F with $f = k_1 F$ and C constant:	$\hat{A} = \dfrac{T_T}{(1/k_1) + Ct}$	$\dfrac{d\hat{A}}{dF} = 0$	0
	$E_{Nmax} = F\hat{A}y - C\hat{A}td$	$\dfrac{dE_{Nmax}}{dF} = \dfrac{T_T y}{(1/k_1) + Ct}$	+

APPENDIX II
CONTINUED.

Scenario: Independent variable	Dependent variable	Derivative	Sign
3: F with $f = k_1F$ and $C = k_2F$:	$\hat{A} = \dfrac{T_T}{(1/k_1) + k_2Ft}$	$\dfrac{d\hat{A}}{dF} = \dfrac{-T_Tk_2t}{((1/k_1) + k_2Ft)^2}$	$-$
	$E_{Nmax} = F\hat{A}y - k_2F\hat{A}td$	$\dfrac{dE_{Nmax}}{dF} = \dfrac{(T_T/k_1)(y - k_2td)}{((1/k_1) + k_2Ft)^2}$	$+$ or $-^c$
4: F with $C = k_2F$ and f constant:	$\hat{A} = \dfrac{T_T}{(F/f) + k_2Ft}$	$\dfrac{d\hat{A}}{dF} = \dfrac{-T_T}{F^2((1/f) + k_2t)}$	$-$
	$E_{Nmax} = F\hat{A}y - k_2F\hat{A}td$	$\dfrac{dE_{Nmax}}{dF} = 0$	0
5: C with F and f constant:	$\hat{A} = \dfrac{T_T}{(F/f) + Ct}$	$\dfrac{d\hat{A}}{dC} = \dfrac{-T_Tt}{((F/f) + Ct)^2}$	$-$
	$E_{Nmax} = F\hat{A}y - C\hat{A}td$	$\dfrac{dE_{Nmax}}{dC} = \dfrac{-T_TFt(y + (d/f))}{((F/f) + Ct)^2}$	$-$

[a] The derivative is positive because $Fy > Ctd$, which is true because $\hat{A}Fy = E_a > E_c = \hat{A}Ctd$ by definition (see Appendix I).

[b] The derivative is positive if the actual daily gross energy gain (E_f) plus the actual daily net energy gain (E_{Nfix}) is greater than the potential gross energy gain of spending the entire day feeding (T_Tk_1Fy), and vice versa (see Fig. 2).

[c] The derivative is positive if the food is relatively energy-rich (y is large) and defense costs per intruder are relatively low (k_2td is small), such that $y > k_2td$, and vice versa.

[d] The derivative is negative because $E_{Nfix} < T_Tfy$, which is true because $E_{Nfix} = T_Tfy - T_c(fy + d)$ by definition (see Appendix I).