Notes and Comments

The Logic of Territory Choice: Implications for Conservation and Source-Sink Dynamics

Hanna Kokko,[1,2,*] William J. Sutherland,[3] and Rufus A. Johnstone[1]

1. Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, United Kingdom;
2. Institute of Biomedical and Life Sciences, Division of Environmental and Evolutionary Biology, University of Glasgow, Glasgow G12 8QQ, United Kingdom;
3. School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, United Kingdom

Pen and Weissing (2000) present an extension and critique of our model (Kokko and Sutherland 1998) of evolutionarily stable habitat usage strategies. In these models, options of floating and queuing are considered in addition to accepting to breed on a territory. We are delighted to see this work, which extends our territory choice model in many fruitful ways. Pen's and Weissing's model describes populations in which there is a specific season for territory acquisition, as, for example, in migratory birds, whereas our model assumed that vacancies can be created and filled at any time of the year so that high-quality breeding habitat is constantly in short supply. Our assumption applies, for example, to many cooperatively breeding species that defend their territories year-round. Pen's and Weissing's analysis shows that some important aspects of our results are substantially modified by the incorporation of seasonality into the model. In particular, we note that seasonally limited territory acquisition has a strong effect on the extent to which sink habitats are used: the evolutionary equilibrium in our aseasonal model predicts that individuals should always avoid areas in which lifetime reproductive success falls below unity, whereas

* Corresponding author; e-mail: h.kokko@bio.gla.ac.uk.

breeding may occur in sinks, to some extent, in the seasonal environment modeled by Pen and Weissing.

However, we take issue with the Pen's and Weissing's (2000) larger claim that it is premature to draw general conclusions relevant to conservation biology from models of territory choice. In our original article (Kokko and Sutherland 1998), we showed that the evolutionarily stable solution of our model maximized the number of nonbreeding individuals. Pen and Weissing argue that this result is not robust to the details of the model assumptions since incorporation of seasonality (and the consequent possibility to choose between several territories simultaneously) eliminates this relationship. We accept that this is the case in seasonal environments, which were not included in our original model (Kokko and Sutherland 1998); however, we wish to point out that a closely related and more general maximization relation holds for both models and, indeed, for further variations on the original analysis.

In Pen's and Weissing's "free floating" case, the number of floaters is maximized at $\mathrm{LRS}(x) = 1$, that is, when only source habitats are used for breeding, whereas the evolutionarily stable strategy (ESS) criterion is $\mathrm{LRS}(x^*) = 1 - \mu_F$ (see table 1 for definition of variables). Here, they fail to notice that x^*, itself, has interesting properties: it will maximize the number of individuals n_C that compete in spring for the available territories. These are either survived floaters or newly produced offspring. Applying equations (A1), (A2), (A3), and (A6) of the appendix of Pen and Weissing (2000) and noting that $u_F(x^*)/u_B(x^*) = n_F/n_B$ at equilibrium, we obtain the number of competitors:

$$n_C = (1 - \mu_F)n_F + \overline{F}n_B$$

$$= \frac{C}{\mu_F}\left[\int_{x^*}^{\infty} F(q)p(q)dq - (1 - \mu_F)\int_{x^*}^{\infty} \mu_B(q)p(q)dq\right].$$

Applying the fundamental theorem of calculus gives us

Table 1: List of variables and their definitions

Variable	Definition
C	Total number of available territories
$F(q)$	(Yearly) rate of production of surviving offspring in territories of quality q
$p(q)$	Probability density (i.e., relative number) of territories of quality q
n_C	Number of individuals that compete for territories
n_F	Number of breeders
$\text{LSR}(x)$	Lifetime reproductive success in a territory of quality x
μ_F	Mortality of floaters
$\mu_B(q)$	Mortality of breeders when breeding in a territory of quality q
x	Acceptance threshold for territory quality
x^*	Evolutionarily stable acceptance threshold

Note: Notations follow that of Pen and Weissing (2000). Notations such as $\overline{F}(x^*)$ and $\bar{\mu}_B(x^*)$ refer to values averaged across territory qualities of x^* or higher.

$$\frac{dn_C}{dx^*} = \frac{Cp(x^*)}{\mu_F}[(1 - \mu_F)\mu_B(x^*) - F(x^*)],$$

which implies that the maximum of n_C is obtained when $\text{LRS}(x^*) = F(x^*)/\mu_B(x^*) = 1 - \mu_F$. This is exactly the value that Pen's and Weissing's (2000) analysis shows to be the ESS. Thus, the ESS maximizes the number of competitors for the limited resource (here, competitor numbers in the spring), rather than those who temporarily fail to acquire a territory (floaters in the summer). In our original aseasonal model (Kokko and Sutherland 1998), these are equivalent, as the pool of floaters provides the continuous competition for territories; hence, the aseasonal model maximizes floater numbers as a special case of a more general maximization principle.

Indeed, maximization of such a buffer of surplus competitors for a resource can be shown to hold in further variations of territory choice models. As an example, we may relax the common assumption made both by Kokko and Sutherland (1998) and Pen and Weissing (2000) that territories are chosen for life and, instead, assume that every individual chooses the best possible territory in each season but leaves it after the breeding season (as, e.g., in migratory birds). Such a model assumes that there are no opportunity costs of acquiring a territory. While the complete absence of such costs is unlikely, as some site tenacity occurs in many migratory species, this assumption is useful, as it provides an extreme contrast to Kokko and Sutherland (1998) and Pen and Weissing (2000), where results were based on opportunity costs. We may, instead, consider a survival cost of breeding by setting $\mu_B(q) > \mu_F$ at least for territories of low-quality q. With no opportunity costs, it is sufficient to calculate the payoff from a single breeding attempt; it exceeds that of floating simply whenever

$$F(q) + [1 - \mu_B(q)] > 1 - \mu_F$$

$$\Leftrightarrow F(q) > \mu_B(q) - \mu_F,$$

that is, when the expected production of offspring, $F(q)$, exceeds the mortality cost $\mu_B(q) - \mu_F$ that breeding imposes on the parent. Thus, the lifetime reproductive success at birds breeding at territories of threshold quality must satisfy $\text{LRS}(x^*) = 1 - \mu_F/\mu_B(x^*)$. Assuming iteroparity ($\mu_B(x^*) < 1$), this is always less than the threshold $1 - \mu_F$ by Pen and Weissing, that assumed opportunity costs due to lifetime site tenacity once a territory has been chosen. Thus, low-quality habitats (which correspond to sinks if maturation occurs at age 1) are used for breeding if there are no opportunity costs and to an even greater extent than in the model of Pen and Weissing (since $1 - \mu_F/\mu_B(x^*) < 1 - \mu_F < 1$). A similar calculation to that above shows that this x^* again maximizes the number of spring competitors, which now equals the size of the whole population:

$$n_C = n_B + n_F$$

$$= C\left(\frac{\int_{x^*}^{\infty} F(q)p(q)dq - \int_{x^*}^{\infty} \mu_B(q)p(q)dq}{\mu_F} + \int_{x^*}^{\infty} p(q)dq\right).$$

The criterion for the maximum becomes

$$-\frac{F(x^*)p(x^*)}{\mu_F} + \frac{\mu_B(x^*)p(x^*)}{\mu_F} + p(x^*) =$$

$$\left[\frac{\mu_B(x^*) - F(x^*)}{\mu_F} + 1\right]p(x^*) = 0$$

The bracketed term becomes 0 when $\mu_B(x^*) - F(x^*) = -\mu_F$, which implies that the maximum of the number of

competitors, n_C, must have $LRS(x^*) = F(x^*)/\mu_B(x^*) = 1 - \mu_F/\mu_B(x^*)$. This matches the ESS criterion above.

It is less clear whether this maximization principle also holds for queuing for single territories, and we appreciate the complications that Pen and Weissing (2000) point out in this context. However, considering the simulated queuing scenario presented by Pen and Weissing, the number of queuers is clearly largest near the value $LRS(x^*) = 0.6$ that they find optimal (fig. 1). This appears to support the existence of similar buffering effects even in the presence of stochastic mortality and reproduction, which take account of the necessarily discrete length of queues. We find similar results with other choices of numerical examples for $\mu_B(q)$ and μ_F.

Hence, the aseasonal model of Kokko and Sutherland (1998), the seasonal model of Pen and Weissing (2000), and the costly breeding model outlined above, do not produce conflicting results. They apply to different situations regarding timing and the nature of costs of territory acquisition. Moreover, they all appear to be examples of a more general principle of buffering: in populations limited by site availability, habitat selection maximizes the size of the population stage that is competing for territories. This, in turn, is an example where a central result of life-history theory is applied to populations regulated by site availability: in temporally stable populations, natural selection acting on life- history traits will maximize the number of individuals in the stage that is subject to density dependence (Charlesworth 1980, p. 168). This result assumes one-dimensional population regulation: in all the models discussed, regulation operates via declining offspring production as lower-quality habitats become occupied.

Contrary to Pen's and Weissing's claim (2000, p. 514) that "Kokko and Sutherland's model does not allow for ideal habitat selection," all the models discussed here are based on the principle of ideal habitat selection, set in a dynamic context. The apparently indiscriminate use of territories above the threshold quality in our original (Kokko and Sutherland 1998), aseasonal case simply reflects the fact that in a population where suitable territories remain occupied throughout the year, such territories become vacant one at a time. Ideal habitat selection and setting of a simple acceptance threshold for territory quality are thus indistinguishable and fully compatible. It is only in nonequilibrium populations—which are not considered in Pen's and Weissing's analysis at all—that the distinction becomes significant (and, as we pointed out in our original article [Kokko and Sutherland 1998, p. 359], ideal selection is then favored over indiscriminate habitat choice).

Thus, while the details of the process of territory acquisition may differ among models (and among populations), we claim that consequences for conservation ecol-
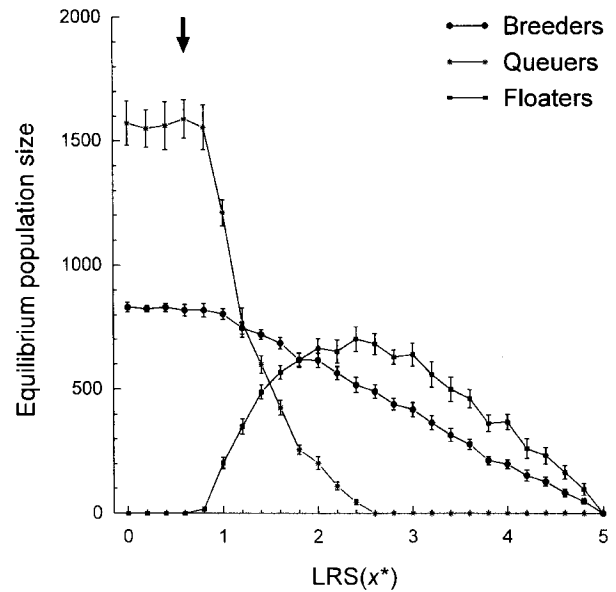

Figure 1: Simulation of a queuing system with demographic stochasticity. Equilibrium population sizes (mean and standard error of 20 replicates, each comprising the last 25 generations of 100 generations simulated population dynamics) are given for floaters, queuers, and breeders with $\mu_B = 0.2$, $\mu_F = 0.4$, and LRS of 1,000 territories varying between 0 and 5 as in Pen and Weissing (2000, p. 514). Queuers and breeders have equal mortality, and offspring number from each territory is a Poisson random variable with mean $F(q) = \mu_B LRS(q)$. With an evolving threshold x^*, we find evolution toward $LRS(x^*) \approx 0.6$ (marked with arrow) as in Pen and Weissing (2000); the evolutionary trajectory is similar to Pen's and Weissing's figure 4 and is not shown here. Compared with alternative values of $LRS(x^*)$, this produces a maximum number of queuing individuals. However, we also note that values of $LRS(x^*)$ lower than 0.6 produce effectively the same outcome: here, the breeding and the queuing populations become limited by low offspring production in the worst territories, rather than having limited access to acceptable territories. Thus, even a zero threshold ($LRS(x^*) = 0$) does not predict that all 1,000 territories become occupied, and at equilibrium, new queuers do not, in practice, end up in queues with LRS < 0.6.

ogy are more robust. Conservationists often argue in terms of "suitable" habitat for a species, without recognizing that suitability may be a graded property and also subject to evolutionary decisions. Combining ideal habitat selection with floating options shows how individually optimal waiting behavior may lead to some of the habitat remaining unused even if it were of high enough quality to contribute to population persistence at least to some degree. Natural selection makes individuals avoid sinks (or too detrimental sinks, depending on the nature of breeding costs and the age at first breeding), even though a breeder in sink habitat could contribute more to population growth than the same individual merely competing to replace other individuals in the source. For example, Komdeur (1996) describes

floater behavior in the Seychelles magpie robins *Copsychus sechellarum*, a species that was, until recently, confined to a single island in the Seychelles. Only part of this island qualifies as breeding habitat, and surplus birds float and harass breeders instead of attempting to breed in low-quality habitat. This had an adverse effect on reproduction in an extremely endangered population (17–21 birds in 1988–1990), and translocations of floaters to the nearby island of Aride have led to a clear increase in global population size. Our modeling suggests that the evolutionary self interest of individuals may often result in suboptimal behavior from a conservation point of view, and human intervention that encourages more breeding to take place may be necessary in extreme cases.

A perhaps more commonly applicable result of our models is that the buffer population of floaters, or queuers, is often large and contributes significantly to total population size. This fraction of the population will respond differently to habitat loss than the breeding population. Our original conclusions regarding the consequences of habitat loss hold for all three of the models we have mentioned: our original analysis (Kokko and Sutherland 1998), the seasonal model of Pen and Weissing, and the costly breeding model. Regardless of the precise assumptions made regarding order and timing of territory acquisition, we can expect stronger population responses in the buffer than in the breeding population, if habitat of above-average quality is lost (fig. 2). This result is based on the simple assumption that better habitats have higher productivity (so that the loss of one breeding pair results in a greater impact on the population, if that pair was breeding in a high-quality territory), and it is thus likely to be very robust. Hence, the common practice of documenting population declines by concentrating solely on numbers of breeding individuals may often underestimate the true decline.

We therefore conclude that models of territory choice can and do yield general conclusions that are relevant to conservation biology. The current discussion shows that it also offers new insight to the evolution of source-sink dynamics, which has obviously important conservation consequences (Pulliam 1988; Pulliam and Danielson 1991; Dias 1996). Breeding in sink habitats has been previously explained as a result of abiotic control of dispersal (Diffendorfer 1998), as sampling error (Székely 1992), as temporary occupation before moving to a better habitat (Morris 1991), or as an allocation strategy in temporally varying environments (Holt 1997; Jansen and Yoshimura 1998). Based on the work of Pen and Weissing (2000), and ourselves, the temporal pattern of territory acquisition—that is, seasonality—may also have surprising and profound effects on the usage of sink habitat.
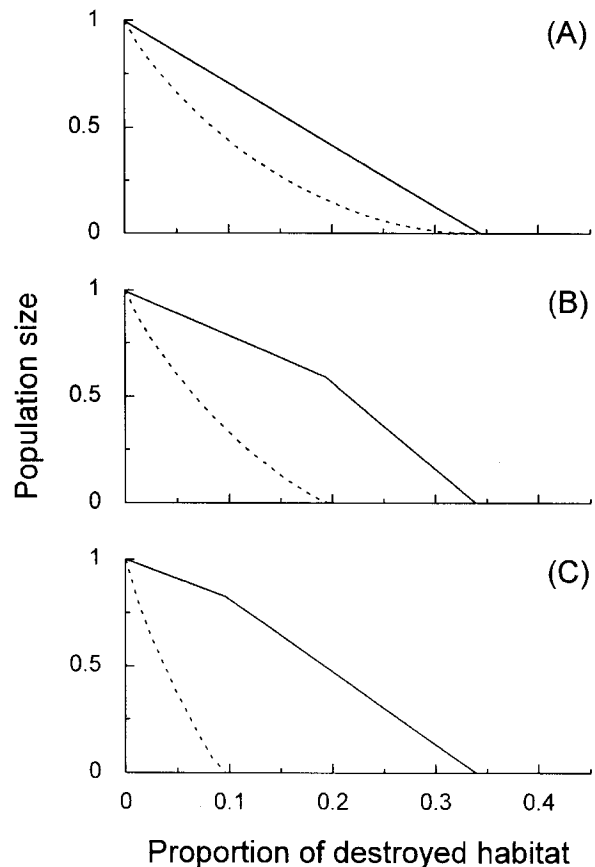

Figure 2: Population responses to habitat loss in three different circumstances: assuming either (*A*) continuous territory acquisition and lifetime territory choice (Kokko and Sutherland 1998), (*B*) seasonal territory acquisition and lifetime territory choice (Pen and Weissing 2000), or (*C*) seasonal territory acquisition and territory choice each year (the breeding cost model of this note). Habitat destruction starts from best habitats, and solid and dashed lines denote responses of breeding and floating populations relative to their initial sizes, respectively. Parameters used are $\mu_B = 0.6$, $\mu_F = 0.3$; that is, breeding incurs survival costs. The quality distribution of territories $f(R)$—corresponding to $p(q)$ in Pen's and Weissing's more general formulation—follows that of figures 2–4 in Kokko and Sutherland (1998). Ideal habitat selection is assumed, such that in cases where total reproductive output in habitats between x^* and the best existing habitat does not suffice to produce enough individuals to fill all territories in these habitats, populations fill the best fraction of the available habitat until reproduction balances mortality; that is, habitat is in use if $R \geq x$, where x satisfies $\int_x^\infty Rf(R)dR = \mu_B\int_x^\infty f(R)dR$. The floater population decreases more dramatically than the breeder population in all three cases.

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