

Site fidelity in habitats with contrasting levels of nest predation and brood parasitism

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ABSTRACT

The phenomenon of site fidelity (i.e. remaining faithful to sites where an individual has bred successfully in the past) has been documented for many taxa, especially birds. It has been suggested that individuals may use a simple rule of thumb: stay (or return) if breeding was successful, or switch to a new site if breeding was unsuccessful (win-stay/lose-switch; WLS). Using simulations, I examined the evolutionary dynamics of the WLS strategy in competition with two alternative strategies: stay-always (SA; total site fidelity) and two forms of an ideal-free settlement strategy (IFS; site indifferent). I considered two habitats identical in all respects except that one habitat (low quality) had a higher level of nest predation than the other. Between breeding seasons, females: (1) remained in a habitat if they successfully bred or otherwise dispersed to the alternative habitat (WLS); (2) remained in the habitat regardless of their breeding success (SA); or (3) settled within habitats such that the quality of the highest ranking unoccupied territory was equalized, when possible, across habitats (IFS). The WLS strategy invades and replaces either of the alternative strategies. I then examined the consequences of the WLS strategy on population density and mean fecundity across two habitats that had contrasting levels of nest predation or brood parasitism. Unlike contrasting predation rates between habitats, higher levels of brood parasitism in the low-quality habitat rapidly drained away individuals from the better habitat. This result, however, depended both qualitatively and quantitatively on differences (or the lack thereof) in predation between the two habitats. A second invasibility analysis conducted on populations experiencing contrasting brood parasitism between habitats indicated that the WLS resists invasion by the SA strategy but not the IFS strategy. The IFS strategy resists invasions by either alternative. Thus cowbird brood parasitism may rapidly drain individuals away from high-quality habitat because birds cannot discriminate between low- and high-quality habitats. Furthermore, parasitism alters the evolutionary dynamics of competing site fidelity strategies.

Keywords: brood parasitism, evolutionarily stable strategy, habitat selection, metapopulation, nest predation, site fidelity, songbirds.

INTRODUCTION

Individuals generally inhabit environments that are temporally and spatially heterogeneous (Chesson and Rosenzweig, 1991; Hairston *et al.*, 1997; Schmidt *et al.*, 2000). Habitats vary in

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quality for various reasons. For breeding passerines, habitats may differ in vegetative structure (Whelan, 2000), the quality of nesting sites (Shields *et al.*, 1988), the abundance or quality of food resources (Rodenhouse and Holmes, 1992; Sillett *et al.*, 2000), or the level of inter- or intraspecific competition (Nilsson, 1987; Sherry and Holmes, 1988). Nest predation is the principal cause of nesting mortality in songbirds (Ricklefs, 1969; Martin, 1992) and another important source of heterogeneity in habitat quality (Potts *et al.*, 1980; Nilsson, 1987; Morse and Robinson, 1999). Similarly, brood parasitism by the brown-headed cowbird (*Molothrus ater*) may have a severe impact on reproductive success and is likewise heterogeneous in time and space (Brittingham and Temple, 1983; Robinson *et al.*, 1995a).

When habitats vary in quality and individuals cannot immediately or accurately assess potential fitness differences, they may use their past reproductive success as a measure of site quality. Past reproductive success has been demonstrated to influence individuals' future habitat selection (Greenwood and Harvey, 1982; Shields *et al.*, 1988; Switzer, 1997). Site fidelity is the phenomenon of remaining faithful to an area, often breeding locations in which an individual has bred successfully. Site fidelity is known for many taxa (Greenwood and Harvey, 1982; Switzer, 1993, 1997); in particular, it has received much attention among ornithologists (Blancher and Robertson, 1985; Gavin and Bollinger, 1988; Bollinger and Gavin, 1989; Beletsky and Orians, 1991; Haas, 1998).

Imagine sites that retain, on average, their relative qualities over time, but which also have unpredictable or indeterminate spatial variability. Individuals might respond by staying in sites where reproductive success is high, but leaving sites where reproductive success is low (Shields *et al.*, 1988). The simple rule-of-thumb, win-stay/lose-switch rule (WSLS; Shields *et al.*, 1988), has been frequently supported by empirical studies among birds and other taxa (see references above). Individuals (often females) using the WSLS rule are faithful to breeding sites or habitats if their previous breeding attempt was successful (i.e. fledged young); otherwise, they switch to a new habitat.

The WSLS rule may not be adaptive if birds suffer brood parasitism. For instance, adults whose nests have been parasitized may not re-nest after they have successfully fledged young, either their own or primarily cowbird chicks (Pease and Grzybowski, 1995). Thus, birds whose nests have been parasitized may incorrectly assess a location's (e.g. site, territory, habitat) quality if they equate high quality with successfully fledging a brood or measure quality by the numbers of chicks fledged or raised to independence. In contrast, nest predation represents a more 'honest signal', since sites with higher rates of nest predation are indeed of lower quality, all else being equal.

Site fidelity influences metapopulation dynamics because it regulates dispersal between sub-populations. Here I explore a simple model to examine the population consequences of birds that exhibit site fidelity towards habitats where they have successfully fledged young. Specifically, I wish to address the consequences of birds using the simple decision rule, win-stay/lose-switch, under contrasting rates of nest predation or brood parasitism between two habitats. I first consider the evolutionary dynamics of the WSLS in competition with alternative site fidelity strategies. The stay-always strategy (individuals always faithful to their breeding habitat) performed better than the WSLS in previous theoretical analyses (Switzer, 1993) and has some empirical support (Krebs, 1971; Bédard and LaPointe, 1984). A second alternative strategy that I develop below, the ideal-free settlement strategy, considers individuals that equalize (when possible) their expected fecundity between habitats. Finally, I demonstrate that the evolutionary dynamics of site fidelity strategies may also depend on the specific cause of reproductive failure.

MODELLING SITE FIDELITY

Imagine that birds settle into one of two habitats that differ in quality in terms of the risk of nest predation. We might expect birds to minimize the risk of predation by choosing a habitat with, for example, adequate vegetation cover, but structural characteristics are often unrelated to nest predation rates (Filliater *et al.*, 1994; Braden, 1999; Schmidt and Whelan, 1999b; Misenhelter and Rotenberry, 2000). Furthermore, predator density is also often unrelated to nest predation rates (Reitsma *et al.*, 1990; Schmidt, 1999; Schmidt *et al.*, in press) or predator densities cannot be assessed (e.g. Pöysä *et al.*, 2001), particularly when predators are nocturnal. Indeed, there are very few examples, outside of colonial seabirds, indicating that birds settle disproportionately in sites with fewer nest predators (for a song-bird example, see Jędrzejewski and Jędrzejewska, 1998). Given this uncertainty, how does a bird choose which is the better habitat?

To address this question, I constructed a model consisting of two populations connected to each other through juvenile dispersal and dispersal of adults that are unfaithful (i.e. do not return the following year) to one habitat or the other between breeding seasons. I assume that population fecundity is density-dependent. This is probable when high-quality territories are selected earliest as individuals settle into their breeding habitat, and successively filled territories are of increasingly poor quality (Rodenhouse *et al.*, 1997; for examples, see Krebs, 1970; Potts *et al.*, 1980; Wauters and Dhondt, 1990; Dhondt *et al.*, 1992). Thus, once a habitat is chosen, birds may sample territories and choose the one with the highest expected fecundity (e.g. with high insect abundance). However, I assume that nest predation rates cannot be assessed through sampling either within or between habitats.

For simplicity and to allow a greater control over the shape of the relationship, I assume that instantaneous fecundity (i.e. the quality of the next available site) declines exponentially with population density:

$$F_1 = a[e^{-b(N/2)}] \quad (1)$$

The terms a and b are constants that set the maximum possible fecundity in the habitat (when population density is zero; $N = 0$) and the rate of decline in fecundity with increasing population density, respectively. Population density is divided by 2 to reflect density dependence in the number of nesting pairs. Thus, the model assumes a 1:1 sex ratio and that all birds are paired with mates. It further assumes that breeding pairs will not form a territory when the expected fecundity drops below < 0.5 young per nest-attempt. This truncates the maximum breeding density. However, under realistic adult and juvenile annual survivorship, simulated populations did not reach densities at which territories became limiting.

Mean fecundity, F_M , declines with density and can be computed from the integral of equation (1) for a density of $(N/2)$ breeding pairs as:

$$F_M = [1/(N/2)][-(a/b)e^{-b(N/2)} + (a/b)e^{(0)}] \quad (2)$$

This formulation assumes that territories are sequentially filled in the order of highest to lowest expected fecundity. Realized mean fecundity is determined by multiplying equation (2) by P , the probability a given pair successfully breeds. This probability is in turn determined from the probability a given nest will be preyed upon and by the number of nesting attempts. I compute this probability as $P = 1 - Pr^3$, where Pr is the probability of nest predation on any one nest-attempt. This formulation assumes that birds are single brooded

and allows up to two re-nesting attempts (maximum of three total nest-attempts) following predation (see Schmidt and Whelan, 1999a).

Population density is determined by adult and juvenile survivorship over the non-breeding season, their fidelity patterns and the production of offspring from the previous year. Population density for the high-quality habitat in year t is:

$$N_H(t) = S_A[A_H(t-1)\lambda_H + A_L(t-1)(1-\lambda_L)] + S_J[P_H F_{M,H} A_H(t-1) + P_L F_{M,L} A_L(t-1)]/2 \quad (3)$$

Note that the invasibility simulations shown below required following populations of individual fidelity strategies separately due to differences in site fidelity, λ , and then summing densities in a given habitat to calculate mean fecundity using equation (2). S_A and S_J are the adult and juvenile survival rates, respectively, λ is the proportion of the adult population that is site faithful, and the subscripts H and L denote high- and low-quality habitat, respectively. Returning juveniles disperse evenly between the two habitats and hence their density is divided by 2. (This makes the assumption that the habitats are of equal size. I later discuss potential consequences of relaxing this assumption.) For all simulations using the WSLS strategy, I also assume that site fidelity is equivalent to the probability of successfully fledging young during the breeding season (i.e. $\lambda = P$). Thus individuals remain more faithful to sites with the lower nest predation rates. However, site choice does not depend on brood parasitism (included later) or on the number of young fledged. In other words, fidelity – or, more correctly, its converse, infidelity – is a response to qualitative differences in nesting success rather than quantitative differences in productivity. Whether individuals use experience gained from single or multiple predation/nesting events to assess habitat quality is an intriguing question, but is beyond the scope of the present study. Finally, individuals may of course move around within a habitat either within or between breeding seasons as a response to poor territory quality; such behaviour would not reduce the generality of the current model.

Settlement rules

In this section, I compare the invasibility of three different settlement strategies: win-stay/lose-switch (WSLS), stay-always (SA) and two ideal-free settlement (IFS) strategies. Stay-always strategists settle randomly across habitats following natal dispersal and return to the same habitat to breed each year. An individual using the SA strategy has perfect site-fidelity: $\lambda = 1$. Individuals using the IFS strategy are site indifferent. Ideal-free settlement strategists settle evenly across habitats following natal dispersal, but as adults they settle into habitats such that the expected fecundity of the next highest ranking available territory (i.e. at the time of settlement) is equal between habitats. Therefore, an individual could not benefit were it to change habitats. In this sense, the IFS is similar to the ideal-free distribution, the latter representing the evolutionarily stable distribution of individuals between habitats (Fretwell and Lucas, 1970; Brown, 1998). I included the IFS strategy since birds using it are making, at the time of settlement, an apparently adaptive decision, and thus IFS may be evolutionarily favoured over alternative strategies.

I investigated two forms of the IFS strategy: predator-naive and predator-omniscient. The predator-naive strategy attempts to equalize the expected instantaneous fecundity between the habitats *exclusive* of the probability of nest predation. This case may be appropriate when birds cannot assess predator densities or risk differences between habitats. The predator-omniscient strategy attempts to equalize the expected instantaneous fecundity

between habitats *inclusive* of the probability of nest predation. For either strategy, for each simulated time step (see below), I used the Goal Seek function in Excel to determine the proportion of adults in the IFS population that must be present in the high-quality habitat to equalize expected instantaneous fecundity, when possible. Because the omniscient form recognizes differences in quality between the two habitats due to predation risk, population densities differ between the habitats in the absence of the WSLs strategy (Fig. 3), whereas the naive strategy treats the two habitats as identical (Fig. 2).

Invasibility analyses

I simulated populations that consisted of a pure strategy (SA or IFS) and determined whether a rare mutant invader using the WSLs strategy could invade a population of SA or IFS strategists. For all simulations discussed in this paper, I set survivorships at $S_A = 0.70$ and $S_J = 0.35$, typical of many passerines (Nolan, 1978; Roth and Johnson, 1993; Simons *et al.*, 2000). Similarly, maximum fecundity was set at $a = 4.2$ and the decline in fecundity at $b = 0.06$. I set the density of the mutant strategy in the low-quality habitat to 0.10 and ran ≥ 1000 generations to determine if one of the strategies went extinct (i.e. density < 0.001). For invasibility analyses, nest predation was 0.50 and 0.80 in the high- and low-quality habitats, respectively, and brood parasitism was absent. I also verified the invasibility results for all simulations under conditions of stochastic nest predation rates (pulled from a uniform distribution with a range of ± 0.10 around the mean value used in the non-stochastic simulations). In general, stochastic predation lengthens the time required for invasion to be completed, but does not alter the qualitative outcomes. Therefore, I do not discuss these simulations further.

The WSLs strategist invades a system of pure stay-always strategists (Fig. 1). Given a SA strategy at equilibrium, the distribution of expected fitness of individuals *inclusive* of the risk of nest predation is identical between habitats, and population densities are equal. However, if habitats differ in their maximum fecundity (parameter a) or its decline with density (parameter b), population density is higher in the better habitat. In either case, the WSLs strategy can invade and replace a pure SA strategy (Fig. 1). The WSLs strategy replaces the SA strategy because WSLs individuals discriminate between low- and high-quality habitat. At equilibrium, the SA strategists have equal density in the two habitats despite the inherent difference in habitat quality (Fig. 1).

Win-stay/lose-switch also invades and replaces a pure IFS strategy whether in its naive form (Fig. 2) or its omniscient form (Fig. 3). As the rare mutant WSLs strategists increase in density, the proportion of IFS strategists using the high-quality habitat decreases until the IFS strategy is restricted to the low-quality habitat (however, juvenile dispersal continues). This occurs because individuals using the IFS strategy (indeed, for any strategy) disperse across the two habitats such that the cumulative growth rate of the IFS strategy is the weighted average of the two populations. However, WSLs individuals are more likely to remain or resettle in the better (i.e. low predation) habitat because adult dispersal from high- to low-quality habitat is more likely than the reverse. Therefore, WSLs strategists passively coerce the 'indifferent' IFS strategists into the poorer habitat. The main difference in the invasion dynamics between the strategies is the rate of replacement (Figs 2 and 3). The WSLs strategy takes four times as many generations to replace the predator-omniscient strategy as the predator-naive strategy. Furthermore, I ran additional simulations in which I varied the absolute difference in predation rates between the two habitats. The above

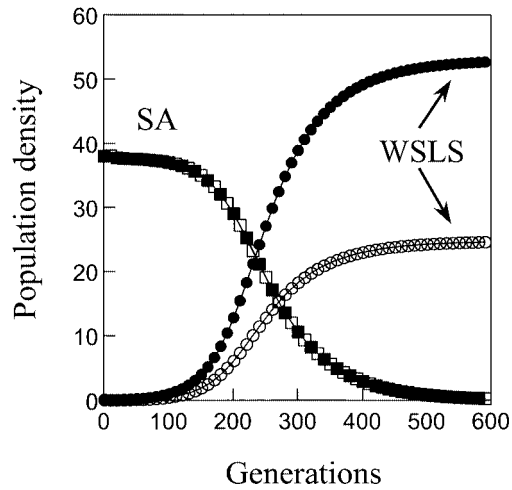


Fig. 1. The win-stay/lose-switch strategy (WLS) invades and replaces the stay-always strategy (SA; squares). Filled symbols denote high-quality habitat ($Pr = 0.50$), open symbols denote low-quality habitat ($Pr = 0.80$). Brood parasitism is absent and predation rates are constant over time. Symbols are given for every 10th year to facilitate viewing.

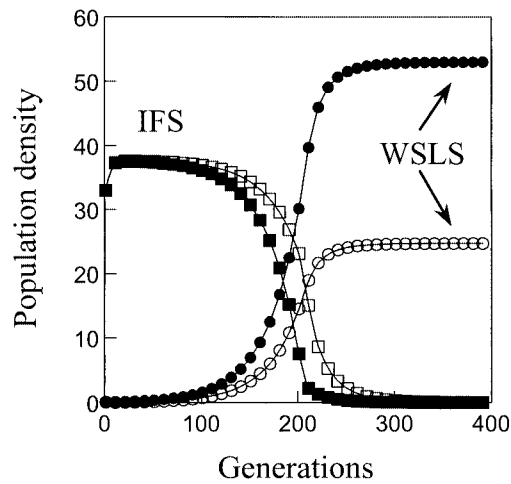


Fig. 2. The win-stay/lose-switch strategy (WLS) invades and replaces the predator-naive IFS strategy (squares). Filled symbols denote high-quality habitat ($Pr = 0.50$), open symbols denote low-quality habitat ($Pr = 0.80$). Brood parasitism is absent and predation rates are constant over time. Symbols are given for every 10th year to facilitate viewing.

results (WLS invades SA or IFS) appear robust to changes in absolute nest predation rates. However, as predation rates in the two habitats become increasingly similar, the rate at which one strategy replaces another becomes increasingly slower.

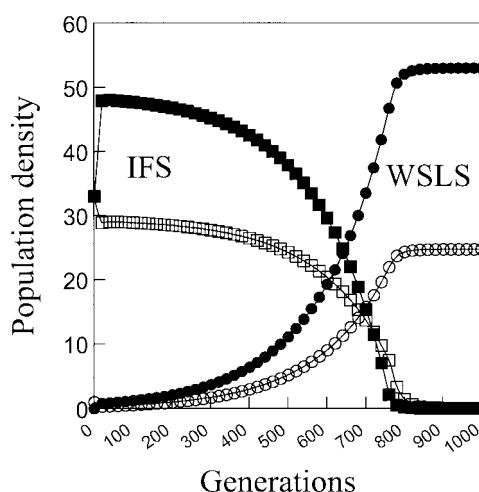


Fig. 3. The win-stay/lose-switch strategy (WSLS) invades and replaces the predator-omniscient IFS strategy (squares). Filled symbols denote high-quality habitat ($Pr = 0.50$), open symbols denote low-quality habitat ($Pr = 0.80$). Brood parasitism is absent and predation rates are constant over time. Symbols are given for every 10th year to facilitate viewing.

The models assume that a strategy's fitness can be represented by the mean fitness of the habitat. In particular, it assumes that individuals of any two competing strategies settle randomly with respect to the order of occupation of sites, which, in turn, determines the quality of the resulting sites. When a strategy is rare, this may not be true for any given settlement period. However, the results are still instructive because they indicate the probable outcome over a repeated number of settlement periods or potential invasions of one strategy by another. Furthermore, a habitat's mean fitness may not be indicative of a strategy's fitness if individuals retain or otherwise pre-empt high-quality territories that they occupied in a previous year. Such features will probably slow down the dynamics of strategy invasions but not alter the long-term results, since individuals must ultimately give up their territory when they die.

This section is not meant to provide a complete analysis of strategy replacement, but it does indicate that, under some circumstances, the WSLS rule prevails. Thus, it provides a theoretical foundation in support of the empirical demonstrations of a WSLS-type rule (Greenwood and Harvey, 1982; Blancher and Robertson, 1985; Gavin and Bollinger, 1988; Bollinger and Gavin, 1989; Beletsky and Orians, 1991; Switzer, 1993; Haas, 1998). Other factors, especially social, are likely to be involved, such as site incumbency or pre-emption. Whether the results are robust to modifications, such as competition for sites, remains to be seen. In particular, I will consider brood parasitism below.

Population consequences

In this section, I explore the implications of site fidelity, under the WSLS rule, on population dynamics when habitats differ in quality because of differences in either nest predation rates or brood parasitism rates. For predation, I let the high-quality habitat have a constant

predation rate ($Pr = 0.50$) and increased the predation rate in the low-quality habitat by 0.05 increments from 0.50 to 0.95. Brood parasitism was absent. I let the populations equilibrate (100 generations) and determined the population density and mean fecundity for each habitat. In the second model, I assumed predation was constant in either habitat at $Pr = 0.50$ and brood parasitism was non-existent in the high-quality habitat. I then increased the parasitism rate in the low-quality habitat by 0.10 increments from 0.0 to 1.00. Populations experiencing brood parasitism had their fecundity adjusted as $F_M' = F_M[P(1 - PsR)]$, where Ps is the probability any given nest attempt is parasitized, R is the mean reduction (as a proportion) in the expected number of fledglings from a parasitized nest, and P is as before. For the purposes of the figures, I held R constant at 0.67. As in the previous model, I let the populations equilibrate (100 generations) and determined the population density and mean fecundity for each habitat. For either model, I assumed both nest predation and brood parasitism rates were constant throughout the breeding season and were unrelated to the density of nesting pairs.

Habitats with contrasting nest predation rates

As the qualities of the two habitats diverge due to differences in nest predation rates, more individuals settle in the high-quality habitat, in turn depressing the mean fecundity (Fig. 4). In contrast, the decline in density in the low-quality habitat increases mean fitness, despite higher predation rates, through the relaxation of density dependence in fecundity. However, this effect depends both qualitatively and quantitatively on the parameter values chosen. Higher ranking unoccupied territories occur in the low-quality habitat, although differences in predation rates between habitats diminish these differences. All these effects are rather minor and reach their zenith when the low-quality habitat has a 0.60 probability of nest predation (Fig. 4). As predation increases further, the relaxation of density-dependent

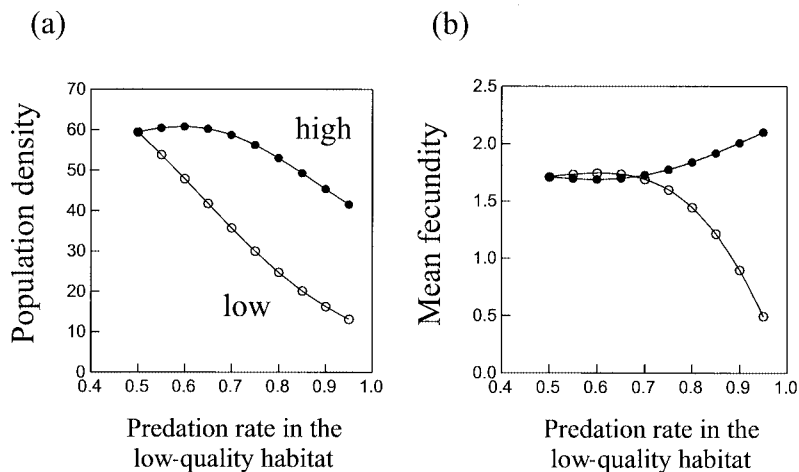


Fig. 4. Population density (a) and mean fecundity (b) for habitats with contrasting nest predation rates and individuals using the WLS rule. The x-axis gives the nest predation rates in the low-quality habitat; predation in the high-quality habitat is constant at $Pr = 0.50$. Solid symbols denote high-quality habitat, open symbols denote low-quality habitat.

fecundity cannot compensate for the loss of juvenile recruits from the low-quality habitat and both habitats experience population declines (Fig. 4a). As predation in the low-quality habitat increases beyond 0.70, mean fitness deviates rapidly (Fig. 4b).

As the population density in the poor habitat decreases as the predation rate rises, mean fecundity shows little effect until $Pr > 0.70$. More importantly, while the density of the high-quality habitat decreases after $Pr > 0.60$, the density never falls below 70% of its level at $Pr = 0.50$.

Habitats with contrasting brood parasitism rates

The effects of a difference in brood parasitism rates are in marked contrast to those seen under contrasting predation rates. Brood parasitism causes an immediate decline in population density in both habitats (Fig. 5a) and an immediate divergence in mean fecundity (Fig. 5b). Population densities are identical in the habitats, since birds cannot discern habitat quality when predation rates are identical. Finally, under 100% parasitism, the population densities in each habitat decline to ~35% of their parasitism-free levels (Fig. 5a).

There are two ways of viewing the situation under contrasting predation or parasitism rates. First, one may view the high-quality habitat as ‘rescuing’ the low-quality habitat. Alternatively, the low-quality habitat can be seen as a drain on the high-quality habitat. Regardless, the drain of individuals away from the better habitat is greatest under contrasting parasitism rates.

This effect depends, however, on nest predation rates (Fig. 6). Increasing the predation rate in the habitat with brood parasitism actually increases population densities substantially (Fig. 6b). This occurs because individuals now use the differences in predation rates to correctly assess differences in habitat quality and to determine their site fidelity.

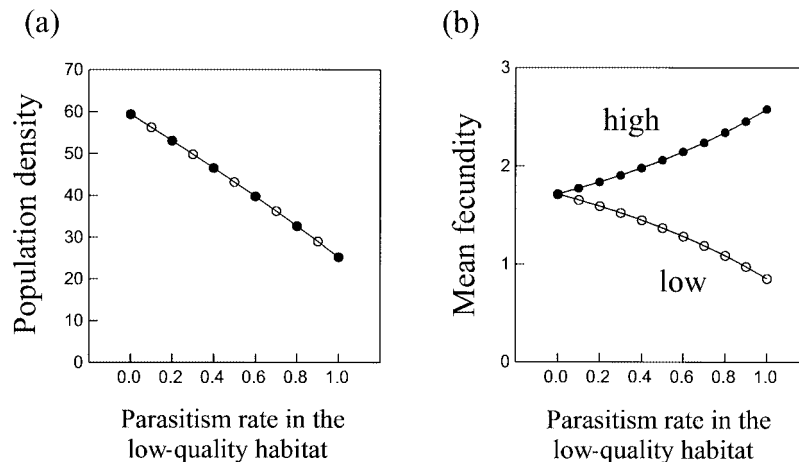


Fig. 5. Population density (a) and mean fecundity (b) for habitats with contrasting brood parasitism rates and individuals using the WLS rule. The x-axis gives the rate of brood parasitism in the low-quality habitat; parasitism in the high-quality habitat is absent. Solid symbols denote high-quality habitat, open symbols denote low-quality habitat.

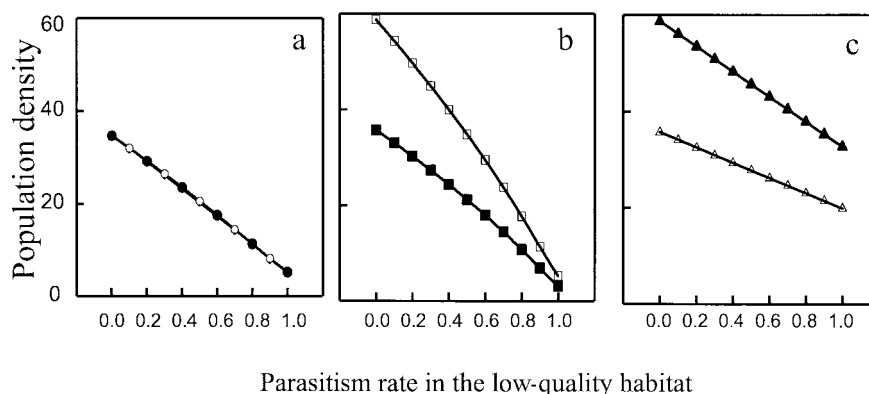


Fig. 6. Population density for habitats with contrasting brood parasitism rates and (a) equal predation rates ($Pr = 0.70$), (b) higher predation in the habitat with brood parasitism (with parasitism, $Pr = 0.70$; without parasitism, $Pr = 0.50$) and (c) lower predation in the habitat with brood parasitism (with parasitism, $Pr = 0.50$; without parasitism, $Pr = 0.70$). Individuals use the WLSL rule. Solid symbols denote high-quality habitat, open symbols denote low-quality habitat.

Individuals bias their habitat use away from the poor habitat and, in turn, away from brood parasitism. Of course, higher predation rates in the habitat without brood parasitism have the opposite effect (Fig. 6c).

Evolutionary dynamics under contrasting brood parasitism

Treating two habitats that experience contrasting brood parasitism rates as equivalent is intuitively non-adaptive. To explore this, I conducted a second invasibility analysis similar to the one described earlier, but using populations experiencing (1) contrasting rates of brood parasitism ($P_s = 0.0$ versus $P_s = 0.70$, $R = 0.67$) but identical rates of nest predation ($Pr = 0.50$), and (2) contrasting rates of both brood parasitism and nest predation (high quality: $P_s = 0.0$, $Pr = 0.50$; low quality: $P_s = 0.70$, $R = 0.67$, $Pr = 0.80$).

As in the earlier model, the WLSL strategy may invade and replace the SA strategy (Fig. 7; shown for the scenario of stochastic predation rates). But replacement occurs only when nest predation rates vary between the habitats. Because site fidelity is related to the rate of nest predation, under equal predation rates the two strategies experience each habitat equally and thus the WLSL and SA strategies are indistinguishable. Equilibrium densities depend on the rates of nest predation and brood parasitism and the initial starting densities. Interestingly, when nest predation in the habitat with high brood parasitism is reduced below that in the habitat without brood parasitism, the SA strategy can invade and replace the WLSL strategy. This occurs for the reasons I have already noted (Fig. 6): the higher nest predation results in a greater proportion of individuals leaving the habitat without brood parasitism in the WLSL strategy relative to the SA strategy.

In sharp contrast to earlier results, both IFS strategies (predator-naive and predator-omniscient) invade and replace the WLSL strategy when populations experience contrasting levels of brood parasitism (Fig. 8; shown for the predator-naive IFS). This result does not depend on whether populations had equal or contrasting levels of nest predation.

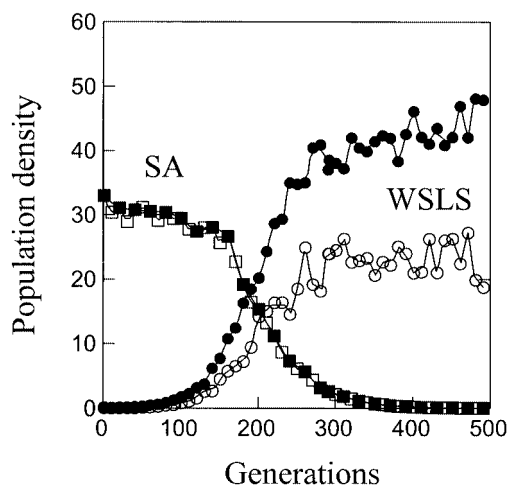


Fig. 7. The win-stay/lose-switch strategy (WSLS) invades and replaces the stay-always strategy (SA; squares). Filled symbols denote high-quality habitat (parasitism absent), open symbols denote low-quality habitat ($P_s = 0.70$, $R = 0.67$). Nest predation is stochastic but is, on average, lower in the high-quality habitat (0.50 vs 0.80). Symbols are given for every 10th year to facilitate viewing.

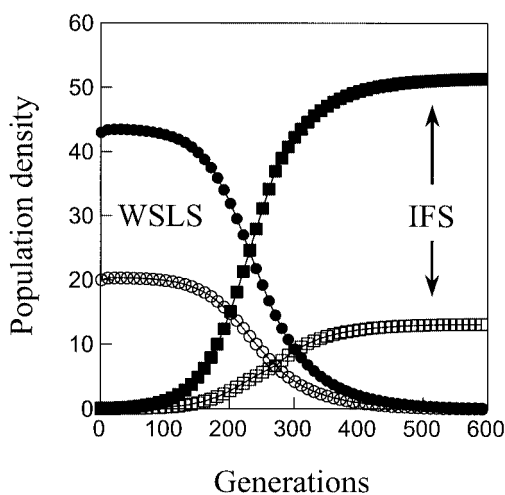


Fig. 8. The predator-naive IFS strategy (squares) invades and replaces the win-stay/lose-switch strategy (WSLS). Filled symbols denote high-quality habitat (parasitism absent), open symbols denote low-quality habitat ($P_s = 0.70$, $R = 0.67$). Symbols are given for every 10th year to facilitate viewing.

DISCUSSION

The decision to remain faithful to sites where an individual has bred successfully (i.e. fledged young) in the past, but to disperse from sites in which breeding was unsuccessful, is adaptive under some scenarios investigated here. In particular, in the absence of brood parasitism,

the WSLS strategy is able to invade and replace strategies that are either completely site faithful (stay-always) or site indifferent (IFS strategy). In competition with these alternative strategies, WSLS is evolutionarily stable. This may explain why win-stay/lose-switch is commonly observed among a variety of taxa (Greenwood and Harvey, 1982; Shields, 1984; Blatcher and Robertson, 1985; Gavin and Bollinger, 1988; Bollinger and Gavin, 1989; Beletsky and Orians, 1991; Switzer, 1993; Haas, 1998), although rarely in the ideal form as modelled here. Nest predation is largely unpredictable and strongly determines fecundity, and thus fitness, in birds. The WSLS strategy may have evolved to enable individuals to bias their reproductive efforts towards those habitats in which reproductive success is high, but unpredictable in time or space.

Recent analyses have questioned the adaptiveness of the win-stay/lose-switch decision rule despite frequent empirical examples (see earlier citations). Switzer (1993), for instance, showed that the WSLS rule often performed considerably worse than the optimal fidelity strategy as determined by dynamic programming. In that study, the stay-always decision rule generally performed as well as or better than the WSLS rule, particularly when habitats were unpredictable. However, Switzer's model did not incorporate density dependence in fecundity. On the other hand, the present model does not incorporate costs of switching between habitats. Making it costly to switch between habitats would tend to retain individuals that would otherwise be unfaithful to a site. If switching costs are severe enough, it is probable that the SA strategy would resist invasion by alternative strategies. Density dependence, therefore, appears critical to maintaining the WSLS strategy. Alternative forms of density dependence, such as the level of nest predation (Schmidt and Whelan, 1999c), have not been explored but do warrant consideration.

With the population explosion of brown-headed cowbirds in the last century (Mayfield, 1977; Robinson *et al.*, 1995a), songbird populations have been mildly to severely impacted (Robinson and Wilcove, 1994; Robinson *et al.*, 1995a,b; Payne and Payne, 1998; Trine, 1998). However, the negative influence of cowbirds on lifetime fecundity may be greater than previously considered. For instance, breeding songbirds that experience cowbird parasitism may raise successful broods, but these broods often contain fewer of their own young (Robinson *et al.*, 1995a; Trine, 1998). If birds with parasitized nests use the act of fledging to assess habitat quality, they may remain faithful to low-quality sites and thus bias their breeding effort towards habitats that have high or even average fledging success, but low host reproductive success. Alternatively, birds may use the number of young raised from a territory or nest. In this case, whether the above results hold may depend on whether the total number of host and non-host fledglings or juveniles increases or decreases with brood parasitism, and on whether or not adults can distinguish their young from cowbird young and act on this assessment. These are unexplored empirical issues.

When site fidelity is determined by the act of fledging young, the effects of brood parasitism are more or less extended to all sub-populations, even to those populations that do not experience brood parasitism (Figs 5 and 6). The ability of birds to bias reproductive effort away from the poorer habitat depends on whether and how predation rates differ between habitats (Fig. 6). Population densities can quickly decline in the metapopulation as a whole as parasitism increases in any one habitat, although when both parasitism and predation covary positively, the effect is ameliorated. When populations experience contrasting levels of nest predation alone, the effect is relatively insignificant until the sub-populations diverge substantially in their predation rates (Fig. 4). Even then, because

the population biases reproductive effort towards high-quality habitat, the magnitude of the decline in density is much reduced relative to the brood parasitism scenario.

It is not surprising that the WLSL strategy, which performs poorly under contrasting levels of brood parasitism, is not evolutionarily stable in these circumstances. While site fidelity in response to predation rates or reproductive success has received much attention, site fidelity in response to brood parasitism rates has, to my knowledge, been relatively unexplored. Payne and Payne (1998) did not study site fidelity *per se*, but did find that parasitized female indigo buntings were just as likely as non-parasitized females to return to their study sites in the next season. I do not have the data to determine whether birds are in fact faithful to sites where they have successfully raised a reduced brood through the effects of brood parasitism. My results suggest that parasitized populations should not use the WLSL strategy, but this strategy is the most likely to have evolved before populations had experienced substantial cowbird parasitism. The slow rate of replacement in strategies, gene flow between populations that experience different levels of brood parasitism, and evolutionary lag (Rothstein and Robinson, 1994) will probably slow the evolutionary dynamics of strategy replacement. Despite the strong effects of cowbird parasitism on some songbird species, not all susceptible species have developed anti-parasitism strategies (Rohwer and Spaw, 1988; Rothstein, 1990).

Implications for fragmented habitats

The model proposed here assumes only two habitat types, that there is only one patch of each and that they have the same size. Such habitat patches may represent cases with many discrete habitat patches that are equally common and have equal size. The model ignores patch configuration and patch distribution in space, each of which may have important consequences for population dynamics (Wiegand *et al.*, 1999). However, for simplicity, we may ask if there are natural circumstances that mimic the structure of the model. Habitat fragmentation is one possibility. For instance, small forest fragments have high nest predation and brood parasitism rates, and one may suspect that these fragments are coupled to larger forest blocks with low nest predation and low brood parasitism (Robinson *et al.*, 1995b; Simons *et al.*, 2000). Treating such a complex scenario will require at least two additional considerations: (1) habitat size is related to fecundity (Hoover *et al.*, 1995; Weinberg and Roth, 1998) and (2) forest fragments may be more abundant than large forest blocks (e.g. Robinson *et al.*, 1995b; Heske *et al.*, 1999). Building such a model is beyond the scope of the present study, but some potential results are intriguing. For instance, imagine a scenario where the number of territories in low-quality habitat exceeds the number in high-quality habitat, because of an abundance of smaller forest fragments. The amount of high-quality habitat may be insufficient to sustain populations in low-quality habitats. Furthermore, populations in high-quality habitat may be reduced significantly by the emigration of individuals into low-quality habitats. These results are not new (Pulliam and Danielson, 1991; Wiegand *et al.*, 1999), but the current analysis suggests that the quantitative relationship between the minimum ratio of good: poor habitat that can sustain a metapopulation may depend both on the causes of low reproductive success and the site fidelity strategy that individuals use. In general, the role of site fidelity in metapopulation dynamics is a relatively unexplored issue (but see Villard *et al.*, 1995) that may be critical for assessing the impacts of processes such as habitat fragmentation.

CONCLUSIONS

In the face of global climate change and species introductions or invasions, songbirds, and indeed most organisms, are currently experiencing novel environments. Behavioural rules of thumb, such as the WSLs rule, that were once adaptive, may no longer benefit individuals or populations inhabiting these changed or changing environments. Since the spread of cowbird populations throughout the United States and Canada, ornithologists have documented the negative influences of cowbirds on songbird populations. However, these costs may be more cryptic than previously considered and may influence not only population dynamics in time, but also alter the evolutionary dynamics of species' behaviour. In the absence of evolutionary responses to cowbird parasitism, songbird populations may be less well equipped to persist in parasitized landscapes.

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