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NEGATIVE MATERNAL OR PATERNAL EFFECTS ON TACTIC INHERITANCE UNDER A CONDITIONAL STRATEGY

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Abstract.—Alternative behavioral and life-history tactics are common in animal populations. The conditional strategy model provides a powerful explanation for the evolution and persistence of such tactics, as it allows alternative tactics to be perpetuated even if there is tactic inheritance and tactics yield unequal mean fitness. In many biological systems negative maternal or paternal effects complicate the inheritance of condition and, hence, the inheritance of alternative tactics. Indeed, the inheritance of condition may result in the alternation of tactics across generations. In this paper, we show that the conditional strategy is robust to these effects on progeny condition. There is a unique and stable proportion of tactics under standard inheritance and unequal tactic fitness, and these two important properties of the conditional strategy hold even if negative maternal or paternal effects on progeny condition cause tactics to alternate across generations. However, the dynamics of tactic proportions pursuant to a perturbation of the equilibrium tactic proportions depend on the form of tactic inheritance. An application of our theoretical results to data from a population of smallmouth bass (*Micropterus dolomieu*) in which negative paternal effects dictate progeny condition reveals that age at first reproduction in males alternates regularly across generations. Furthermore, the model indicates that the population would return rapidly to equilibrium if the proportions of males that mature early or late in life were perturbed from the equilibrium within the system. This example shows how the model of the conditional strategy can be used to gain insight into tactic dynamics in situations where some of the model parameters are difficult or impossible to measure empirically.

Key words.—Alternative tactics, game theory, life history, smallmouth bass, tactic alternation.

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The expression of life-history tactics often depends on the condition of an individual, which implies that there will be inheritance of tactics whenever condition is itself heritable (Gross and Repka 1998a). However, the perpetuation of alternative tactics is problematic in this situation because tactics rarely yield equal fitness (Bell 1997; Roff 1997). If there is inheritance of tactics and tactic fitness is unequal, then selection is expected to eliminate inferior tactics from a population (Maynard Smith 1982; Parker 1982; Charnov 1993; Repka and Gross 1995). The fact that tactic diversity is relatively commonplace consequently requires explanation (reviewed by Gross 1996).

The problem of inheritance of condition-dependent tactics and unequal tactic fitness was recently resolved in a model of the conditional strategy (Repka and Gross 1995; Gross and Repka 1998a,b). In this model, a decision mechanism directs individuals into alternative tactics, and the mechanism that guides individuals into tactics that yield the highest fitness for their condition becomes fixed in the population. In the model of the conditional strategy the strategy is the genetic mechanism that codes for tactic choices. Repka and Gross (1995) showed that there is a unique, equilibrium proportion of tactics in this situation, even if tactics are heritable and tactic fitness is unequal. This equilibrium proportion is also stable—a perturbation of tactic proportions results in the return of proportions to the equilibrium (Gross and Repka 1998a). Thus, the conditional strategy allows for the persistence of a unique, equilibrium proportion of alternative tactics within a population.

Repka and Gross (1995) and Gross and Repka (1998a,b) modeled a situation in which males adopt one of two tactics, α or β, based on their condition, where males of high condition adopt the α tactic and males of low condition adopt the β tactic. They assumed that males that adopt the α tactic produce proportionately more progeny that in turn adopt the α tactic than do males that adopt the alternative β tactic, as their goal was to show that neither tactic need be eliminated from a population if tactics are heritable and also yield unequal fitness. However, the problem of tactic inheritance and the persistence of alternative tactics in a population is further complicated by negative maternal or paternal effects that cause progeny to express the opposite condition of their parents (see Kirkpatrick and Lande 1989). Under the conditional strategy model negative maternal or paternal effects may result in the production of a higher proportion of α progeny by β parents than by α parents (Wiegmann et al. 1997). In this situation, the inheritance of condition causes the alternation of tactics across generations, a pattern that appears to occur in several fishes and other animals (Bilton 1971; Dickerson et al. 1974; Tsukamoto et al. 1987; Janssen et al. 1988; Baylis et al. 1993; Wiegmann et al. 1997).

In this paper, we examine how negative maternal or paternal effects influence the two important properties of the conditional strategy, namely the uniqueness and stability of tactic proportions. We show that the model of the conditional strategy is robust to negative maternal or paternal effects on progeny condition, although the dynamics of tactic proportions depend on the pattern of tactic inheritance. We also use the model to estimate boundaries on tactic inheritance and the frequency of tactic alternation in a natural population.

CONDITIONAL STRATEGY WITH NEGATIVE PATERNAL EFFECTS ON TACTIC INHERITANCE

Repka and Gross (1995) showed that there is a unique, equilibrium proportion of two condition-dependent male tactics, α and β, even if tactics are heritable and tactic fitness is unequal. Gross and Repka (1998a) later showed that the equilibrium proportion of tactics is also stable—the proportion of tactics returns to the equilibrium if it is perturbed from the equilibrium. In particular, these properties of the conditional strategy were shown to hold when $w_\beta < w_\alpha$ and $0 < i_\beta < p < i_\alpha < 1$, where w_α and w_β are the mean fitness of α and β males, i_α and i_β are the proportion of α progeny produced by α and β males, and p is the proportion of individuals that adopt the α tactic. Here, we show that these two properties of the conditional strategy—a unique and stable equilibrium proportion of tactics—also hold if tactic fitness is unequal and there are negative paternal (or maternal) effects on progeny condition that produce an alternation of tactics across generations.

Like Repka and Gross (1995) and Gross and Repka (1998a), we use the conditional strategy to examine properties of alternative male tactics, but the model can be applied to either sex. Thus, we assume that a negative paternal effect has an influence on the condition of male progeny and, hence, on their expression of tactics. In particular, our goal is to show that there is an equilibrium proportion of the α (and hence β) tactic that is unique and stable when $w_\beta < w_\alpha$ and $0 < i_\alpha < p < i_\beta < 1$. The tactic inheritance relationship $0 < i_\alpha < p < i_\beta < 1$ accommodates a negative paternal effect, where males of high condition produce a lower proportion of high condition progeny than males of low condition. The inheritance of condition in this manner causes tactics to alternate across generations because tactic choice is determined by male condition.

The structure of our proofs follows earlier theoretical work on properties of the conditional strategy (Gross and Repka 1998a). Let p_n equal the proportion of males that adopt the α tactic in generation n. The proportion of males that adopt the α tactic in generation $n + 1$ is then

$$p_{n+1} = [p_n w_\alpha i_\alpha + (1 - p_n) w_\beta i_\beta]/[p_n w_\alpha + (1 - p_n) w_\beta]. \quad (1)$$

Multiplying the numerator and denominator of equation (1) by $1/w_\beta$, we find

$$p_{n+1} = [p_n r i_\alpha + (1 - p_n) i_\beta]/[p_n r + (1 - p_n)], \quad (2)$$

where $r > 1$ is the ratio of α male and β male fitness. This expression reveals that tactic proportions depend on the relative fitness of males that adopt each tactic and not on absolute tactic fitness (see also Gross and Repka 1998a). The proportion of the α tactic is at equilibrium when $p_{n+1} = p_n = p$ so that at equilibrium equation (2) simplifies to

$$p = [p r i_\alpha + (1 - p) i_\beta]/[p r + (1 - p)]. \quad (3)$$

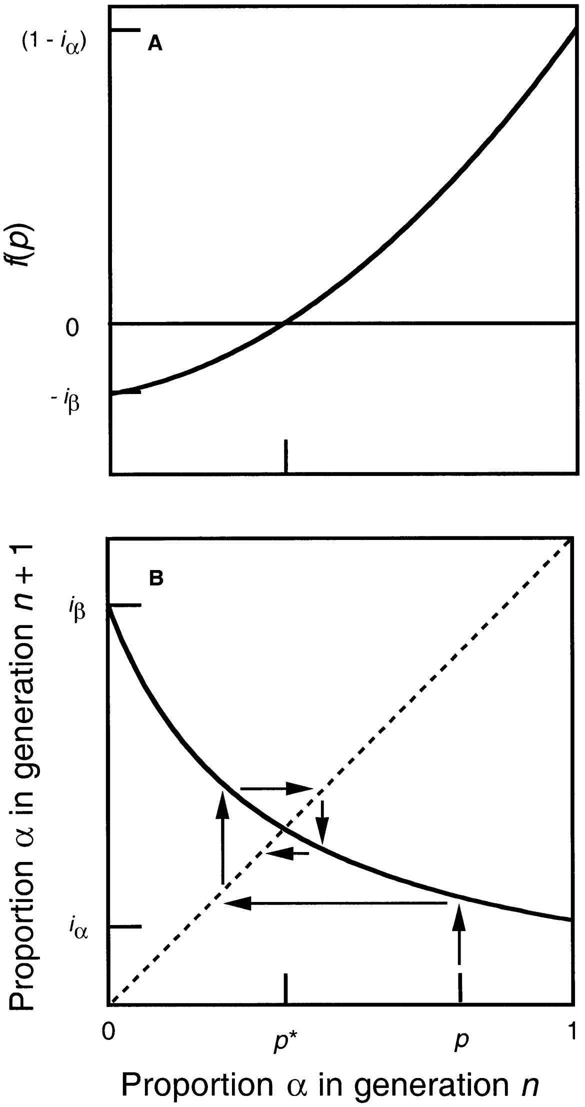

FIG. 1. The equilibrium and stability of tactic proportions under a negative paternal (or maternal) effect on progeny condition. (A) The function $f(p)$ of the parabola given by equation (3) crosses $f(p) = 0$ only once between $p = 0$ and $p = 1$, which establishes that there is a unique equilibrium proportion of the α (and hence β) tactic. (B) The relationship between p_{n+1} and p_n, as given by equation (2), is shown pursuant to a perturbation of p from the equilibrium. The proportion of males that adopts the α tactic oscillates above and below p^* across generations. The dashed diagonal line corresponds to $p_{n+1} = p_n$ and the lines with arrows show the trajectory of the α tactic proportion from an arbitrary initial value of p. The proportion converges on p^* for any initial value of p, which reveals the stability of the equilibrium.

The population is at equilibrium for all p that satisfy this equation.

Rearrangement of equation (3) gives the function $f(p)$ of the parabola

$$f(p) = (r - 1)p^2 + (1 - r i_\alpha + i_\beta)p - i_\beta = 0. \quad (4)$$

The coefficient of p^2 is positive (because $r > 1$) and the parabola opens upward from a negative value of $-i_\beta$ at $p = 0$ toward the positive value $r(1 - i_\alpha)$ at $p = 1$. The parabola

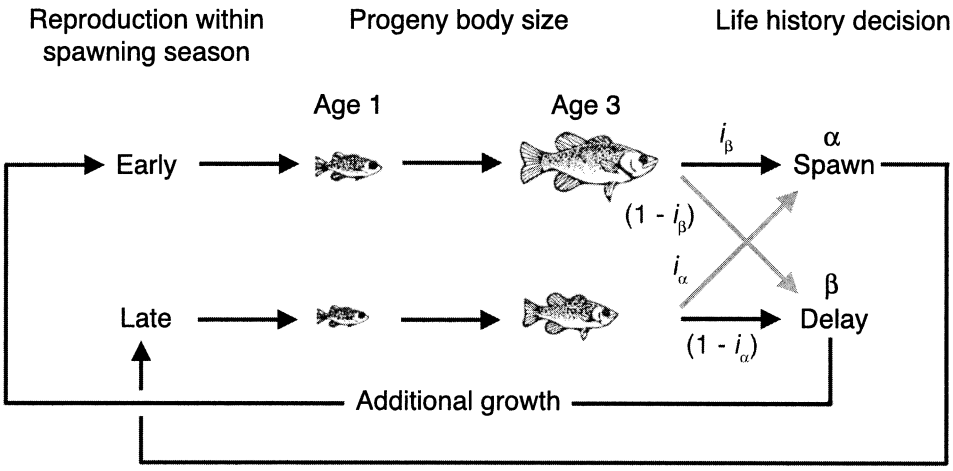

FIG. 2. Life-history alternation in male *Micropterus dolomieu*. Males of a cohort that are large at three years of age adopt the α tactic and spawn, while males that are small adopt the β tactic and delay reproduction. Males that adopt the β tactic continue to grow and ultimately initiate reproduction at a larger body size than males that adopt the α tactic. Males that are large spawn earlier within a spawning season than small males and the progeny of β males consequently have a long period in which to grow in their first year of life, relative to the progeny of α males. Body size differences established at the end of the first year of life are perpetuated until the time of the life-history decision. The inheritance of condition (i.e., body size) results in the alternation (dark arrows) of tactics across generations. The majority of males in the population are semelparous. Adapted from Wiegmann et al. (1997).

consequently crosses the p-axis at only one point between $p = 0$ and $p = 1$, which means that there is only one solution to equation (4) and only one $p = p^*$ that satisfies the equilibrium condition (Fig. 1A). Furthermore, the coefficient of p^2 does not depend on the relationship between i_α and i_β, so there is a unique, equilibrium proportion of the α tactic under the inheritance relationship $0 < i_\alpha < p < i_\beta < 1$ in which there are paternal effects on progeny condition.

The stability of this equilibrium is evident from equation (2), which equals i_β when $p_n = 0$ and i_α when $p_n = 1$. The first derivative of equation (2) with respect to p_n equals $r(i_\alpha - i_\beta)/[p_n r + (1 - p_n)]^2 < 0$. The derivative is negative because $i_\alpha < i_\beta$. The second derivative is $-r(i_\alpha - i_\beta)\{2[p_n r + (1 - p_n)](r - 1)\}/[p_n r + (1 - p_n)]^4 > 0$. Thus, equation (2) decreases with p_n, but the rate of its decrease declines as p_n increases. The curvature of this function causes the stability of the equilibrium p^* (Fig. 1B). If the proportion of males that adopts the α tactic in generation n is lower than p^*, then the proportion in generation $n + 1$ will be higher than p^*, and vice versa, but the curvature of equation (2) guarantees that the absolute difference between p and p^* decreases each generation. Thus, the equilibrium proportion of the α tactic is stable: p returns to p^* if it is perturbed from the equilibrium.

APPLICATION OF THE MODEL

The inheritance of life-history tactics and the prevalence of tactic alternation are not easily measured in field studies. However, the conditional strategy model, applied to two life-history tactics, has only two inheritance parameters, one for each tactic, and three other parameters—w_α, w_β, and p—that are more easily measured in the field. Estimates of these parameters can be applied to the model to determine boundaries on the inheritance of alternative tactics and, hence, on the incidence of tactic alternation (see Gross and Repka 1998a). Here, we apply the conditional strategy model to our earlier work and estimate the frequency of tactic alternation among male smallmouth bass, *Micropterus dolomieu* (Baylis et al. 1993; Baylis 1995; Wiegmann et al. 1997).

Time constraints, like a localized period of reproductive activity, are expected to induce a variable schedule of reproduction among individuals that differ in condition (Rowe and Ludwig 1991; Rowe et al. 1994). In *M. dolomieu* the schedule of reproduction adopted by males depends on body size and, hence, the schedule of reproduction that maximizes fitness presumably varies among individuals based on their condition. In our study population, large males of a cohort spawn at three years of age, while small males delay reproduction (Raffetto et al. 1990; Wiegmann et al. 1992; Baylis et al. 1993). The mean fitness of males that delay reproduction is substantially lower than the fitness of males that spawn early in life, and we consequently refer to the tactics spawn at age 3 and delay reproduction as the α and β tactics, respectively (Wiegmann et al. 1997).

The alternative life-history tactics alternate (to some unknown extent) across generations in this system: males that adopt the α tactic overproduce sons that adopt the β tactic and males that adopt the β tactic produce many sons that adopt the α tactic (Fig. 2; Baylis et al. 1993; Wiegmann et al. 1997). This pattern results because males that adopt the α tactic, although large at the time of the life-history decision, initiate reproduction at a smaller body size than males that delay reproduction. Because body size is negatively related to timing of reproduction within a spawning season, α males spawn later than β males within a season (Turner and MacCrimmon 1970; Ridgway et al. 1991; Wiegmann et al. 1992). The sons of males that adopt the α tactic consequently have a short period to grow before the end of their first year of life relative to the sons of β males (Shuter et al. 1980; Wiegmann et al. 1992). Body size differences of progeny established at the end of their first year of life are perpetuated until the time of the life-history decision, which means that

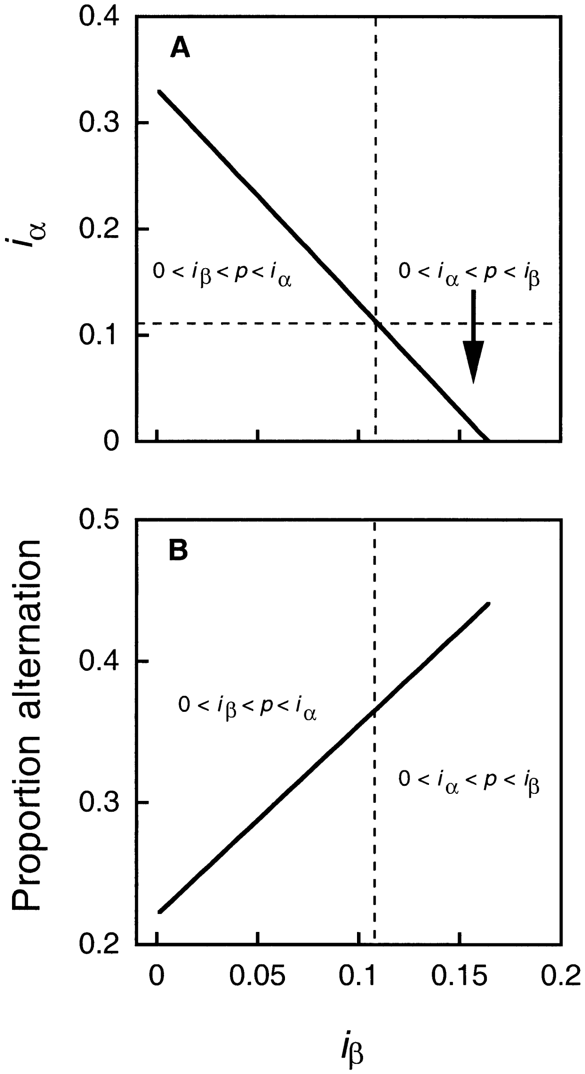

FIG. 3. Inheritance parameters for the α and β tactics. (A) The inheritance parameters that satisfy the equilibrium condition $p^* = 0.11$ and $r = 4$ are shown for $0 < i_\beta < p < i_\alpha < 1$ and $0 < i_\alpha < p < i_\beta < 1$. (B) The frequency of tactic alternation across generations increases as i_α and i_β decrease and increase, respectively. The dashed horizontal and vertical lines correspond to the equilibrium proportion $p^* = 0.11$.

fathers that adopt the α tactic produce sons that are small at age 3 and adopt the β tactic, while sires that delay reproduction produce many sons that are large at age 3 and adopt the α tactic (Baylis et al. 1993; Wiegmann et al. 1997).

Estimates of the proportion of males of a cohort that adopt the α and β tactics and the fitness consequences of these decisions are given in, or are easily derived from, tables provided in an earlier study (Wiegmann et al. 1997). The mean proportion of males of three cohorts that adopted the α tactic was $p^* \pm \mathrm{SE} = 0.11 \pm 0.02$. These males had a mean fitness (i.e., number of eggs in nest) of $w_\alpha \pm \mathrm{SE} = 4506 \pm 982$, while males that adopted the β tactic had a mean fitness of $w_\beta \pm \mathrm{SE} = 1081 \pm 47$. The mean ratio r of α male to β male fitness was $r \pm \mathrm{SE} = 4.2 \pm 1.03$.

These estimates of fitness and the estimate of p^* are sufficient to determine the boundaries on the possible combinations of the two inheritance parameters at equilibrium. The conditional strategy model permits combinations of i_β and i_α where $0 < i_\beta < p < i_\alpha < 1$ or $0 < i_\alpha < p < i_\beta < 1$ (Fig. 3A). However, the inheritance combinations under $0 < i_\beta < p < i_\alpha < 1$ are not consistent with patterns of reproduction within the system; males that adopt the α tactic produce proportionately fewer progeny that adopt the α tactic than males that adopt the β tactic and inheritance of tactics follows $0 < i_\alpha < p < i_\beta < 1$ (Fig. 2). For $p^* = 0.11$ and $r = 4$ the model predicts, in this situation, that the proportion of progeny of α males that adopt the α tactic is $0 < i_\alpha < 0.11$ and the proportion of progeny of β males that adopt the α tactic is $0.11 < i_\beta < 0.16$ (Fig. 3A). The permissible combinations of inheritance parameters under $0 < i_\alpha < p < i_\beta < 1$ imply that the life-history tactic alternates in no less than 0.89 of all progeny of α males and in 0.11 to 0.16 of all progeny of β males. The combinations of tactic inheritances and the observed fitness ratio result in an alternation of tactics in 0.37 to 0.44 of all male progeny each generation when p is at an equilibrium of $p^* = 0.11$ (Fig. 3B).

The importance of inheritance to the dynamics of tactic proportions is evident by an inspection of the response of this system to a perturbation of p from the equilibrium $p^* = 0.11$. If inheritance were $0 < i_\beta < p < i_\alpha < 1$ the return of p to p^* would be monotonic, while the inheritance relationship $0 < i_\alpha < p < i_\beta < 1$, which is consistent with observed patterns of reproduction in the population, causes the tactic proportion p to oscillate about p^* across generations (Fig. 4). If the proportions of α male and β male progeny that adopt the α tactic are each near to p^* the return of p to the equilibrium occurs in a few generations whether $0 < i_\beta < p < i_\alpha < 1$ or $0 < i_\alpha < p < i_\beta < 1$, even if p is perturbed to $p = 0$ or $p = 1$. In contrast, if inheritance parameters are far from p^* the approach of p to the equilibrium is more gradual and the equilibrium condition may not be restored for many generations. In this example, the delay in the return of $p = 0$ to p^* under $0 < i_\beta < p < i_\alpha < 1$ could be as long as 25 generations (Fig. 4B). The tactic proportions are expected to return to equilibrium in no more than approximately five generations under $0 < i_\alpha < p < i_\beta < 1$ (Fig. 4D).

DISCUSSION

The conditional strategy integrates important biological observations that are disallowed by standard game-theory models. In particular, the conditional strategy allows for the persistence of alternative tactics in a population when tactic fitness is unequal and there is heritability of tactics (Repka and Gross 1995; Gross 1996). In this paper, we show that two important properties of the conditional strategy—unique tactic proportions and their stability—are robust to the pattern of inheritance of tactics. There is a unique and stable proportion of tactics even if parents of high condition overproduce progeny of low-condition and parents of low condition produce many progeny of high condition. Such negative paternal (or maternal) effects on progeny condition may often impede selection, as selection for high condition results in the production of low-condition progeny and vice versa (Kirkpatrick and Lande 1989). Negative paternal (or maternal) effects on progeny condition also result in the alternation

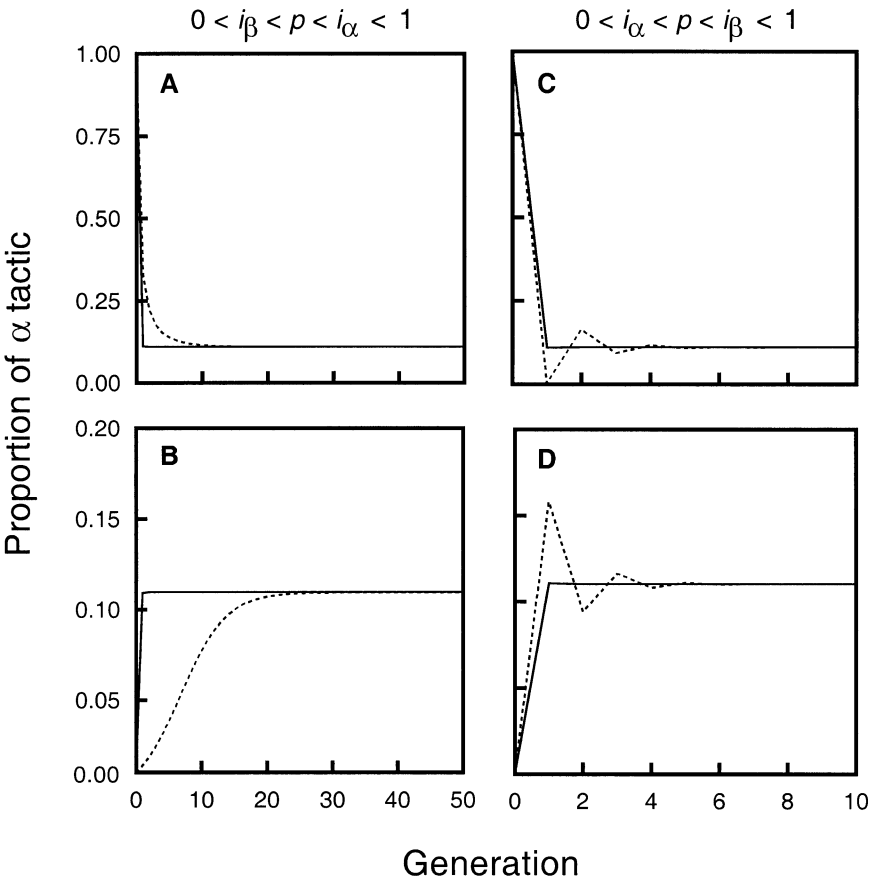

FIG. 4. The dynamics of p over allowable combinations of inheritance of the α tactic. The approach of p to $p^* = 0.11$ from (A, C) $p = 1$ or (B, D) $p = 0$ is shown for $r = 4$ under theoretically permissible combinations of inheritance parameters, where i_α and i_β are as near to p^* (solid curves) or as far from p^* (dashed curves) as allowed by r.

of tactics across generations, but this form of tactic inheritance prohibits neither the uniqueness of tactic proportions nor their stability under the conditional strategy.

The prevalence of tactic alternation in natural populations is difficult to measure, but it appears to occur in a number of organisms (Bilton 1971; Tsukamoto et al. 1987; Janssen et al. 1988; Baylis et al. 1993). The conditional strategy model is constructed of a limited set of parameters, some of which may be easily measured, and information on certain subsets of these parameters is sufficient to derive the others (Gross and Repka 1998b). We used this practical attribute of the model to estimate the inheritance of age at first reproduction amongst male *M. dolomieu*. This life-history decision depends on the body size of an individual, which is itself subject to a negative paternal effect (Baylis et al. 1993; Wiegmann et al. 1997). Inheritance of the α tactic consequently follows $0 < i_\alpha < p < i_\beta < 1$, where the α tactic corresponds to reproduction at a young age and the β tactic corresponds to delayed reproduction. The constraints imposed by $r = 4$ and $p^* = 0.11$ indicate that α and β tactics alternate in more than 0.89 of all progeny of males that adopt the α tactic (as high as 0.16 of progeny of β males) and in up to 0.44 of all male progeny each generation.

The example we chose illustrates the benefit of information on the mechanism of tactic inheritance if these parameters are unknown. The conditional strategy is robust to the precise form of inheritance of tactics and there are combinations of inheritance parameters bounded by either $0 < i_\beta < p < i_\alpha < 1$ or $0 < i_\alpha < p < i_\beta < 1$ that are equally feasible within the theoretical context of the conditional strategy. The response of tactic proportions to a perturbation that shifts p from its equilibrium depends on which of these two inheritance relationships obtains. In our example, the return of p to p^* under $0 < i_\beta < p < i_\alpha < 1$ may be very gradual in comparison to the situation in which $0 < i_\alpha < p < i_\beta < 1$. In general, the dynamics of p are less influenced by the form of inheritance if inheritance parameters are nearly equal to the equilibrium proportion of the α tactic.

The conditional strategy model provides an important explanation for the maintenance of tactic diversity under conditions in which there is heritability of tactics and unequal tactic fitness. In this paper, we showed that the conditional strategy also accommodates negative paternal (or maternal) effects on progeny condition. Under the inheritance relationship $0 < i_\alpha < p < i_\beta < 1$ tactics may regularly alternate across generations, where the frequency of this process depends on p^* and the relative fitness of individuals that adopt each tactic. An application of the model to our study population suggests that age at first reproduction in male *M. dolomieu* alternates at a relatively high frequency across generations, particularly among individuals that adopt the α tactic. Similar applications of the model to other systems may provide useful insights into the dynamics of conditional strategies, where estimates of some of the model parameters are difficult to measure empirically.

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