

## EVOLUTIONARY AND CONTINUOUS STABILITY IN ASYMMETRIC GAMES WITH CONTINUOUS STRATEGY SETS: THE PARENTAL INVESTMENT CONFLICT AS AN EXAMPLE

UZI MOTRO

Department of Evolution, Systematics and Ecology, and Department of Statistics, Hebrew University of Jerusalem, Jerusalem 91904, Israel

*Submitted June 10, 1992; Revised October 14, 1993; Accepted October 29, 1993*

*Abstract.*—In a population that is fixed at an evolutionarily stable strategy (ESS), no mutant strategy can invade and spread. If, however, the strategy set is continuous, one can ask which mutations can be established in a population that is fixed not at an ESS but, rather, at a different, nearby strategy. This question gives rise to a possible distinction between the various ESSs with respect to their dynamic stability characteristics and is treated here for the case of asymmetric games. Two distinct types of ESSs can exist in such games: ESSs that are continuously stable (CSSs) and ESSs that are not. Any strategy in the neighborhood of a continuously stable ESS can always be invaded by mutants that are closer to the ESS. In contrast, any neighborhood of an ESS that is not a CSS contains a nonzero measure set of strategies that are not immune to any mutation that is further away from the ESS. Thus, in natural situations, one can expect more frequently to find populations at (or near) an ESS that is a CSS than at (or near) an ESS that is not continuously stable. The ideas are illustrated by two examples, the parental investment conflict and the dispersal conflict between males and females.

Asymmetric animal conflicts, which are so common in nature, have drawn much attention in the literature. Many game-theory models deal with cases in which the strategy sets include only a finite number (usually two) of pure strategies, with the assumption that the payoff to a mixed strategy is a linear combination of the payoffs to the corresponding pure strategies. Of particular importance in such cases is a theorem by Selten (1980), stating that, as a consequence of any asymmetry that exists between the two players, an evolutionarily stable strategy (ESS) must be a pure strategy; that is, no mixed strategy can be evolutionarily stable in such games. Few works also consider the dynamics of discrete asymmetric games, for example, Gaunersdorfer et al. (1991).

Other works treat continuous asymmetric games, which can be characterized either by having a continuum of pure strategies or by having discrete strategy sets but with payoffs to mixed strategies that are not linear combinations of the payoffs to the corresponding pure strategies. Some examples are the continuous version of the parental investment conflict between males and females (Maynard Smith 1977; Grafen and Sibly 1978; Taylor 1979), the continuous version of the asymmetric war of attrition (Hammerstein 1981; Hammerstein and Parker 1982), a kin selection model of mutual help between relatives having unequal fertilities

(Motro 1988), the begging conflict among chicks in nests that can also be occupied by nest parasites (Motro 1989), the dispersal conflict between males and females (Motro 1991), the parent-offspring conflict and the handicap principle (Eshel and Feldman 1991), the parent-offspring conflict over the sex ratio in a diploid population (Eshel and Sansone 1991), the queen-workers conflict over the sex ratio in the social Hymenoptera (Matessi and Eshel 1992), and others.

The main purpose of this article is to point out a certain aspect of dynamic stability (termed continuous stability), a characteristic that is common to some but not to all ESSs in continuous asymmetric games. The argument is that, in games in which both types of ESSs exist, it is more probable to find the population at (or near) an ESS that is continuously stable than at (or near) an ESS that does not have this property.

The ideas will be demonstrated by two examples. One is a new version of the already-familiar parental investment conflict, and the other is a review of a model considering the dispersal conflict between males and females.

#### EVOLUTIONARY STABILITY AND CONTINUOUS STABILITY

Suppose every contest is between a pair of individuals, one of which is in role *A* (e.g., "male," "older") and the other in role *B* ("female," "younger"). A strategy in such a contest is represented by a pair  $(x, y)$ , where  $x$  ( $x \in S_A$ ) is the strategy adopted if and when the individual is in role *A*, and  $y$  ( $y \in S_B$ ) is the strategy adopted if and when the individual is in role *B*. Following Hammerstein (1981) and Hammerstein and Parker (1982),  $x$  and  $y$  will be referred to as the individual's local strategies in role *A* and in role *B*, respectively. The local strategy sets  $S_A$  and  $S_B$  are assumed to be continuous.

Since we are interested in evolutionary stability, we suppose that the population is fixed at a local *A*-strategy  $x$  and a local *B*-strategy  $y$  and consider the fate of either an *A*- or a *B*-mutant. Thus, let  $W_A(x', x, y)$  be the local payoff to an *A*-mutant, adopting the local strategy  $x' \neq x$  ( $x' \in S_A$ ), and let  $W_B(y', y, x)$  be the local payoff to a *B*-mutant, adopting the local strategy  $y' \neq y$  ( $y' \in S_B$ ), which are introduced into a population that is fixed at  $x$  and  $y$ .

For any given local strategy  $y \in S_B$ , one can ask whether there exists a unique local ESS for *A*, that is, a single strategy  $\hat{x}(y)$  that is immune against invasions by any *A*-mutants. Whenever such a strategy exists, it will be called *A*'s stable reply to the local strategy  $y$  of *B*. Likewise,  $\hat{y}(x)$ , which is the local ESS of *B* (for a given  $x$ ), is *B*'s stable reply to  $x$ . I assume that the stable-reply functions,  $\hat{x}(y)$  and  $\hat{y}(x)$ , are both continuous.

The ESSs of the asymmetric game are represented by the intersection points of the stable-reply curves  $\hat{x}(y)$  and  $\hat{y}(x)$  (provided such intersections exist). Denote such an intersection point by  $(x^*, y^*)$ . Thus, if the population is fixed at  $(x^*, y^*)$ , neither *A*- nor *B*-mutants can invade and spread.

Whereas all intersection points  $(x^*, y^*)$  of the stable-reply curves  $\hat{x}(y)$  and  $\hat{y}(x)$  are stable according to the evolutionary stability criterion (i.e., a population that is fixed at  $(x^*, y^*)$  cannot be invaded either by *A*- or by *B*-mutants), there are intersection points that exhibit an additional form of dynamic stability: a popula-

tion that is fixed at any strategy  $(x^\circ, y^\circ)$  in a neighborhood of such a point can always be invaded by mutants with strategies that are “closer” to the ESS. More precisely, an  $(x^\circ, y^\circ)$  population is not immune either to any  $A$ -mutant with a strategy between  $x^\circ$  and  $x^*$  or to any  $B$ -mutant with a strategy between  $y^\circ$  and  $y^*$  (or may not be immune to any of both). This stronger type of evolutionary stability is a concept similar to that of continuous stability (Eshel and Motro 1981; Eshel 1983), or the equivalent concept of  $m$ -stability combined with  $\delta$ -stability (Taylor 1989) or convergence stability with local ESS stability (Christiansen 1991), which were defined for *symmetric* games with a continuous strategy set. An ESS  $x^*$  of a symmetric game is continuously stable if any population, which is fixed at a nearby strategy  $x^\circ$ , can always be invaded by any mutant with a strategy that is closer to the ESS, that is, by any mutant having a strategy between  $x^\circ$  and  $x^*$ . (While, in the restricted context of linear symmetric games, the original ESS definition of Maynard Smith really embraces the idea of continuous stability [Taylor 1989], evolutionary stability in nonlinear games does not necessarily imply continuous stability.) Although the stronger type of evolutionary stability defined here for asymmetric games is somewhat weaker than continuous stability in symmetric games, I will nevertheless refer to the stronger ESSs of the asymmetric games also as continuously stable strategies (CSSs). In order to avoid confusion, continuous stability in symmetric games will be referred to as one-dimensional continuous stability where necessary.

Suppose that the stable-reply curves are such that, in a neighborhood of an intersection point  $(x^*, y^*)$ , the local ESSs are continuously stable (in the symmetric, one-dimensional sense). That is, for any  $(x^\circ, y^\circ)$  in that neighborhood, an  $(x^\circ, y^\circ)$  population is immune neither to  $A$ -mutants with a strategy  $x$  between  $x^\circ$  and  $\hat{x}(y^\circ)$  nor to  $B$ -mutants with a strategy  $y$  between  $y^\circ$  and  $\hat{y}(x^\circ)$ . A necessary and sufficient condition for an intersection point to be a continuously stable strategy of the asymmetric game can then be geometrically described as follows: At  $(x^*, y^*)$ ,  $\hat{x}(y)$  is an increasing function of  $y$ , while  $\hat{y}(x)$  is a decreasing function of  $x$ , or vice versa. If at  $(x^*, y^*)$  the stable-reply functions are both increasing, then (when viewed in the  $x$ - $y$  plane)  $\hat{y}(x)$  intersects  $\hat{x}(y)$  from above. That is, for all  $y \neq y^*$  sufficiently close to  $y^*$ , the following holds:  $\hat{x}(y) < x^*$  if and only if  $y < \hat{y}(\hat{x}(y))$ . If at  $(x^*, y^*)$  the stable-reply functions are both decreasing or are both flat, then  $\hat{y}(x)$  intersects  $\hat{x}(y)$  from below (see fig. 1A).

If the stable-reply functions are differentiable at  $(x^*, y^*)$ , the condition for continuous stability is that the product of the derivatives satisfies

$$\left. \frac{d\hat{x}(y)}{dy} \right|_{y=y^*} \times \left. \frac{d\hat{y}(x)}{dx} \right|_{x=x^*} \leq 1. \quad (1)$$

In contrast, any neighborhood of the other intersection points always contains a nonzero measure set of strategies that are not immune to both  $x$ -mutants, as well as  $y$ -mutants, that are “further” away from the ESS (see fig. 1B).

Thus, in natural situations, one can expect to more frequently find populations at (or near) a CSS than at (or near) an ESS that is not continuously stable.

To illustrate these ideas, the next sections will consider two examples dealing with conflicts between males and females.

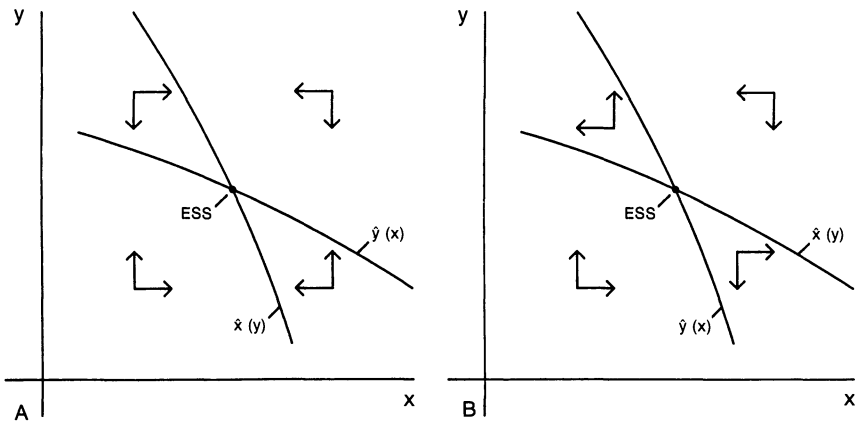


FIG. 1.—Asymmetric ESSs under the assumption that the stable-reply curves are local ESSs that are continuously stable in the relevant one-dimensional symmetric game (see text). *A*, An asymmetric ESS that is also continuously stable; *B*, an asymmetric ESS that is not continuously stable. A population that is fixed on a strategy different from the ESS is not immune to mutations in the directions indicated by arrows.

#### THE PARENTAL INVESTMENT CONFLICT

The question of how much each sex should invest in its own brood has already been treated, as an asymmetric game, by Maynard Smith (1977), Grafen and Sibly (1978), and Taylor (1979). The gene-frequency model presented here is a slightly different version and will also serve to demonstrate the two types of dynamic stability of an ESS. It turns out that, while both types of ESSs (i.e., ESSs that are continuously stable and ESSs that are not) can simultaneously exist in the same game, our parental investment conflict always has an ESS that is continuously stable.

Suppose that there are discrete breeding seasons, and let  $x$  and  $y$  ( $0 \leq x, y \leq 1$ ) be the amount of parental investment (PI) of a female parent and of a male parent, respectively, in each brood. Thus,  $x = 0$  represents absolute neglect, whereas  $x = 1$  denotes a total devotion of the mother in caring for her offspring.

A simple genetic pattern allowing for such sexual differences in the amount of PI is, for example, the existence of two distinct, unlinked autosomal loci responsible for the expression of this trait, only one of which is activated in each individual, according to its own sex.

The expected number of surviving young per brood (EPS, the expected progeny size), which is an increasing function of the amount invested by each parent, is assumed to be a concave function, indicating diminishing returns from parental investment (see, e.g., Maynard Smith 1977). For example, let  $\mu\{1 - \exp[-(x + y + \theta xy)]\}$ , where  $\mu > 0$  and  $\theta \geq -1$ , be the EPS if the female and the male adopt the PI strategies  $x$  and  $y$ , respectively.

The parameter  $\theta$  measures the "interaction" between the two parents. A  $\theta > 0$  indicates that the contributions of the parents are superadditive (i.e., the parents complement each other), in the sense that, if one invests  $x$  and the other invests

$y$ , the expected progeny size of the pair is larger than that of a single parent investing the total of  $x + y$ . (Note, however, that  $\theta > 0$  does not necessarily imply that the EPS of a pair is larger than the sum of EPSs of the two parents had they acted singly.) A  $\theta < 0$  indicates that the contributions are subadditive (i.e., there is some interference between the parents), in the sense that the EPS of a pair, with one parent investing  $x$  and the other investing  $y$ , is smaller than that of a single parent investing  $x + y$ . (This implies that the EPS of a pair is also smaller than the sum of EPSs of the two single parents.) If  $\theta = 0$ , the contributions of the two parents are independent.

As for the parent, the familiar activities of brood care (such as feeding, guarding, and defending the young) involve a loss of energy, an increased risk of predation, and so on. These are likely to decrease the survival probability of the parent. Thus, if a parent that does not invest in parental care has a probability  $q$  ( $0 < q < 1$ ) of surviving to the next breeding season, a parent with a PI strategy  $x$  has only a fraction  $1 - \alpha x$  ( $0 < \alpha < 1$ ) of that probability. I assume that  $\alpha$  is the same for both sexes, which gives rise to an asymmetric game with uncorrelated asymmetry (Maynard Smith and Parker 1976), that is, a game in which the local strategy sets are the same for both roles and the payoff is independent of role ("payoff-irrelevant roles"; Hammerstein 1981). All vacancies, which are the result of this inevitable mortality, are seized by juveniles of the appropriate sex, chosen at random from among the entire progeny of the preceding breeding season.

To find the evolutionarily stable PI strategies, we suppose that the population is fixed at a particular female strategy  $x$  and a particular male strategy  $y$  and consider the fate of a rare, nonrecessive mutation at the female-strategy locus, determining in heterozygotes a female investment strategy  $x' \neq x$ .

Let  $\epsilon_1$  be the frequency of mutants among females of the breeding population, and let  $\epsilon_2$  be the frequency of mutants among males (the mutation is unexpressed in males, so mutant and wild-type males all have the same PI strategy  $y$ ). A fraction  $q(1 - \alpha x')$  of the female mutants and a fraction  $q(1 - \alpha y)$  of the male mutants survive to the next breeding season, compared with  $q(1 - \alpha x)$  and  $q(1 - \alpha y)$  of the female and the male wild type. The proportion of mutants among the juveniles that seize the vacant breeding positions is  $(1/2)(R\epsilon_1 + \epsilon_2) + o(\epsilon_1) + o(\epsilon_2)$ , where  $R = \{1 - \exp[-(x' + y + \theta x'y)]\} / \{1 - \exp[-(x + y + \theta xy)]\}$  and  $o(\epsilon_k)/\epsilon_k \rightarrow 0$  as  $\epsilon_k \rightarrow 0$ . Hence, in the next breeding season, the frequency of mutants among breeding females ( $\epsilon'_1$ ) and the frequency of mutants among breeding males ( $\epsilon'_2$ ) are

$$\epsilon'_1 = \epsilon_1 q(1 - \alpha x') + (1/2)(R\epsilon_1 + \epsilon_2)[1 - q(1 - \alpha x)] + o(\epsilon_1) + o(\epsilon_2) \quad (2a)$$

and

$$\epsilon'_2 = \epsilon_2 q(1 - \alpha y) + (1/2)(R\epsilon_1 + \epsilon_2)[1 - q(1 - \alpha y)] + o(\epsilon_1) + o(\epsilon_2). \quad (2b)$$

The linear approximation matrix of this transformation at  $(\epsilon_1, \epsilon_2) = (0, 0)$  is

$$\Phi = \begin{bmatrix} \partial \epsilon'_1 / \partial \epsilon_1 & \partial \epsilon'_1 / \partial \epsilon_2 \\ \partial \epsilon'_2 / \partial \epsilon_1 & \partial \epsilon'_2 / \partial \epsilon_2 \end{bmatrix},$$

where the derivatives are taken at  $(0, 0)$ . Since all four derivatives are positive, Perron's theorem for positive matrices guarantees that the leading eigenvalue is real and positive. Thus, the stability of  $(0, 0)$  can be determined by examining the sign of  $\Gamma = \det(\Phi - \lambda I)$ . Hence a necessary condition for the stability of  $(0, 0)$  is  $\Gamma \geq 0$ , and a sufficient condition is  $\Gamma > 0$ .

The determinant  $\Gamma$  is a function of  $x'$ ,  $x$ , and  $y$ . Let  $W_F(x', x, y)$  denote the negative value of  $\Gamma$ . Thus,

$$W_F(x', x, y) = (1/2)[1 - q(1 - \alpha y)]\{R[1 - q(1 - \alpha x)] - [1 - q(1 - \alpha x')]\}. \quad (3)$$

(Note that  $W_F(x, x, y) = 0$ .) For any given  $y$ , the female strategy  $x$  is a local ESS if for all  $x' \neq x$ ,  $W_F(x', x, y) < 0$ . (It is worthwhile to note that, in this gene-frequency model, the function  $W_F(x', x, y)$  has a role analogous to that of a payoff function in an ordinary game [see also Motro 1991; Matessi and Eshel 1992].) To obtain the local ESSs, we first solve  $\partial W_F(x', x, y)/\partial x'|_{x'=x} = 0$ , which yields

$$x + y + \theta xy = \log[1 + (\theta y + 1)(x + 1/c)], \quad (4)$$

where  $c = q\alpha/(1 - q)$  is the increase in mortality due to parental care (compared with the mortality without any parental care) and will be called the cost of parental care.

Equation (4) defines  $x$  as a function of  $y$ , which will be denoted by  $\bar{x}(y)$ . By the implicit functions theorem, it can be shown that  $\bar{x}(y)$  is a decreasing function of  $y$  (i.e., the more the males invest in parental care, the less should the females do). Using Eshel's (1983) criterion for continuous stability in symmetric games, we find for each point on the curve  $\bar{x}(y)$  that

$$\frac{\partial^2}{\partial x'^2} W_F(x', x, y) + \frac{\partial^2}{\partial x' \partial x} W_F(x', x, y) < 0. \quad (5)$$

The female's stable reply is

$$\hat{x}(y) = \begin{cases} 0 & \text{if } \bar{x}(y) \leq 0 \\ \bar{x}(y) & \text{if } 0 < \bar{x}(y) < 1 \\ 1 & \text{if } \bar{x}(y) \geq 1, \end{cases} \quad (6)$$

and it is a continuous and decreasing function of  $y$ , the male's PI strategy. The stable-reply curve represents local ESSs that are CSSs of the relevant symmetric game (i.e., one-dimensional CSSs). The ESS property implies that, for any  $y$ , a population that is fixed at a male strategy  $y$  and a female strategy  $\hat{x}(y)$  is immune to any mutant having a female strategy  $x' \neq \hat{x}(y)$ . The one-dimensional continuous stability implies that, if the population is fixed at a male strategy  $y$  and a female strategy  $x^\circ \neq \hat{x}(y)$  but close to  $\hat{x}(y)$ , any mutant with a female strategy  $x'$  that lies between  $x^\circ$  and  $\hat{x}(y)$  has a selective advantage and will spread in that population.

Corresponding features are displayed also by the male's stable reply,  $\hat{y}(x)$ . The ESSs of the asymmetric game are presented by the intersection points of  $\hat{x}(y)$  and  $\hat{y}(x)$ . Thus, if  $(x^*, y^*)$  is such an intersection point, a population that is fixed



at a female strategy  $x^*$  and a male strategy  $y^*$  is immune to mutants having a female strategy  $x \neq x^*$ , as well as to mutants having a male strategy  $y \neq y^*$ .

If the cost of parental care is small enough, that is, if  $c \leq (1 + \theta)/[\exp(2 + \theta) - (2 + \theta)]$ , the stable-reply functions are identically equal to one, yielding the single ESS  $(x^*, y^*) = (1, 1)$ , which is also continuously stable. Thus, for any value of the interaction parameter  $\theta$ , whether positive (indicating that the two parents are complementary), negative (indicating some interference between the parents), or zero, total dedication of both parents to brood care can be evolutionarily stable, provided that the cost of parental care is sufficiently small.

For  $c > (1 + \theta)/[\exp(2 + \theta) - (2 + \theta)]$ , I will distinguish between three different possibilities.

1. *The interaction parameter is larger than the cost of parental care (i.e.,  $\theta > c$ ).*—The stable-reply curves intersect each other at a single point, which is always on the diagonal of the strategy space  $\{(x, y): 0 \leq x, y \leq 1\}$ . Thus, if super-additivity of parental contributions is strong enough, the only ESS is a balanced one (i.e., having  $x^* = y^*$ ), implying that, in an evolutionarily stable population, both sexes should provide equal amounts of parental care.

As expected, the evolutionarily stable PI strategy is a decreasing function of the cost of parental care. At the ESS,  $\hat{x}(y)$  intersects  $\hat{y}(x)$  “from above”; hence the ESS is continuously stable (see fig. 2).

2. *The interaction parameter is smaller than the cost of parental care (i.e.,  $\theta < c$ ).*—In addition to the balanced ESS of the diagonal, which implies equal PI by both parents, the model has two more ESSs, located on the boundaries of the strategy space, having PI strategies that are also decreasing functions of  $c$ .

If  $c > 1/(e - 2)$ , the boundary ESSs are  $(x^*, y^*) = (0, \beta)$  and  $(x^*, y^*) = (\beta, 0)$ , where  $0 < \beta < 1$  is the solution of  $\exp(\beta) - \beta - 1/c = 1$ . In other words, only one of the parents, either the male or the female, takes care of the brood (fig. 3A).

If  $(1 + \theta)/(e - 1) \leq c \leq 1/(e - 2)$ , the boundary ESSs are  $(0, 1)$  and  $(1, 0)$ , that is, while one sex always deserts, the other is fully dedicated to brood care (fig. 3B).

Finally, if  $\theta < c < (1 + \theta)/(e - 1)$ , the boundary ESSs are  $(\gamma, 1)$  and  $(1, \gamma)$ , where  $0 < \gamma < 1$  is the solution of  $\exp[1 + (1 + \theta)\gamma] - (1 + \theta)(\gamma + 1/c) = 1$ . That is, both parents care for the young but not to the same extent; while one sex is fully dedicated to brood care, the other only gives a hand (fig. 3C).

When the model has three ESSs, the balanced ESS of the diagonal is no longer a CSS. Indeed, two regions exist, one in which  $x$  is larger and  $y$  is smaller than the ESS and another in which  $x$  is smaller and  $y$  is larger than the ESS. A population that is fixed at any point  $(x^\circ, y^\circ)$  in these regions is not immune to  $x$ -mutants, as well as to  $y$ -mutants, that are further away from the ESS. In other words, mutations that imply an increased PI by the females, as well as mutations that imply a decreased PI by the males, can all spread in a population that is fixed at an already-female-biased parental investment (and vice versa).

While the balanced ESS is not a CSS, both boundary ESSs are continuously stable. Thus, in such cases, the unbalanced, boundary ESSs are more likely to evolve than the balanced ESS.

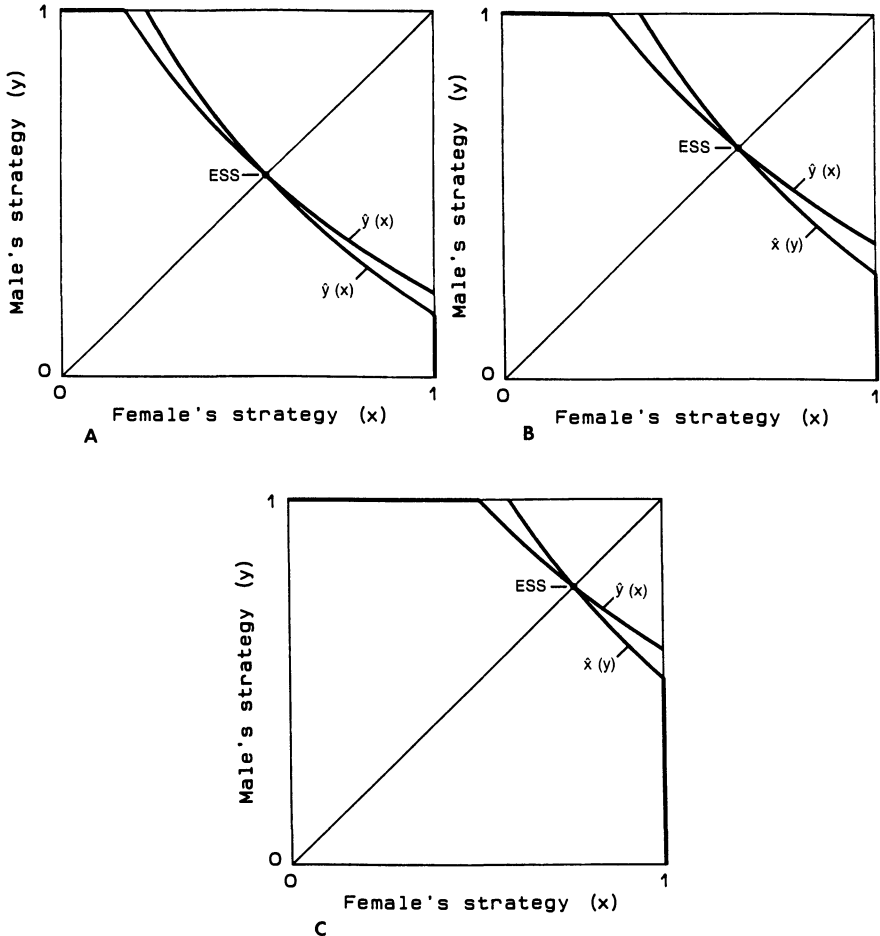


FIG. 2.—The ESS in the parental investment conflict, if the interaction parameter ( $\theta$ ) is larger than the cost of parental care ( $c$ ). A,  $c = 0.7$ ; B,  $c = 0.5$ ; C,  $c = 0.3$  (in each case,  $\theta = 1.0$ ). The single ESS, which is on the diagonal of the strategy space, is continuously stable.

Obviously, the possible existence of three distinct ESSs is not a singular episode, a result of the assumption of uncorrelated asymmetry. If we break the assumption of payoff-irrelevant roles and consider different costs for males and for females, the stable-reply curves will cease to be the reflections of each other with respect to the diagonal of the strategy space. However, if the perturbation is small enough, none of the ESSs will disappear. Thus, while no longer on the diagonal, the inner ESS will retain its non-CSS character. Likewise, the boundary ESSs will both remain continuously stable, but while one implies a larger PI for the parent having the smaller cost (a “commonsense” ESS), the other implies a larger PI for the parent having the larger cost (a “paradoxical” ESS, according to Maynard Smith and Parker 1976; see also Maynard Smith 1982).



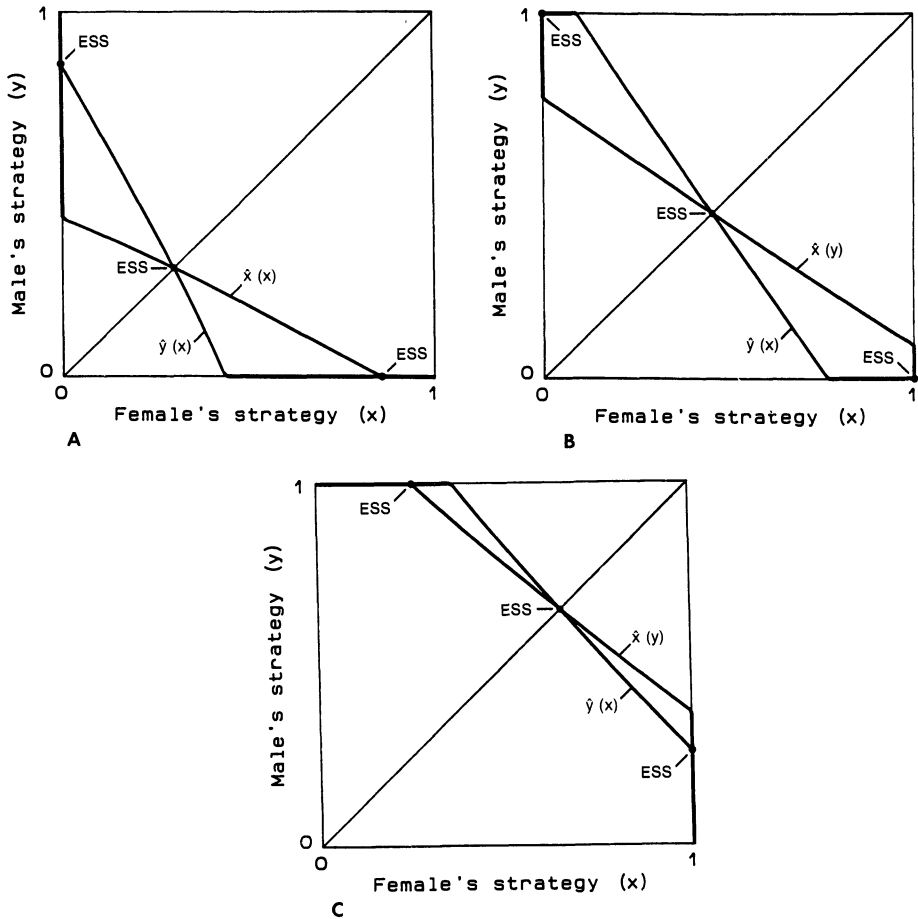


FIG. 3.—The ESSs in the parental investment conflict, if the interaction parameter ( $\theta$ ) is smaller than the cost of parental care ( $c$ ). A,  $c = 2.0$ ; B,  $c = 1.0$ ; C,  $c = 0.5$  (in each case,  $\theta = 0.2$ ). The two boundary ESSs, but not the diagonal ESS, are continuously stable.

3.  $\theta = c$ .—The stable-reply curves coincide in the interior of the strategy space. We thus have a continuum of ESSs, which are all the points of a segment of the hyperbola  $x + y + cxy = \beta$ , where  $\beta$  satisfies  $\exp(\beta) - \beta - 1/c = 1$  and  $\max[0, (\beta - 1)/(1 + c)] \leq x, y \leq \min[\beta, 1]$ .

In conclusion, if the contributions of the two parents are complementary to a large enough extent, that is, if the interaction parameter ( $\theta$ ) is larger than the cost of parental care ( $c$ ), the only ESS is a balanced one and it is continuously stable. The evolutionarily stable PI strategies are decreasing functions of the cost of parental care and imply total dedication to brood care whenever the cost is sufficiently small.

On the other hand, if there is some interference or even if the parents complement each other but not to a large enough extent (i.e., if  $\theta < c$ ), the balanced is

not the only possible ESS. In addition to it, two boundary ESSs also exist, which are continuously stable (whereas the balanced ESS is no longer a CSS). If the cost of parental care is large, the boundary ESSs imply that one of the sexes should desert; if the cost is small, the boundary ESSs imply that one of the sexes should be fully dedicated to brood care; if the cost is smaller yet, the three ESSs coincide, and total dedication of both sexes is then the only ESS.

Similar results have already been obtained by the aforementioned models (Maynard Smith 1977; Grafen and Sibly 1978; Taylor 1979). The model presented here demonstrates, however, that a balanced ESS (i.e., an ESS implying equal PI by both parents) always exists, regardless of whether boundary ESSs exist or not. The balanced ESS is stable according to the evolutionary stability criterion, that is, a population that is fixed at this strategy is immune to invasions by any mutant occurring in either the male or the female strategy. Nevertheless, whenever boundary ESSs do exist, the balanced ESS is not continuously stable; hence, in such cases, it is less likely to evolve.

Furthermore, the stipulation that two parents are not twice as good as one is only a necessary but not a sufficient condition for the existence of boundary ESSs, whereas the stipulation that one parent is less than half as good as two is a sufficient but not a necessary condition for the balanced ESS to be the only ESS (cf. Maynard Smith 1977).

The results of this section can be extended to more general EPS functions (see Appendix). Thus, let the expected progeny size  $F(z)$  be any increasing and concave function of  $z = x + y + \theta xy$  (the effective parental investment), with  $F(0) = 0$ . Then if  $\theta > c$  a balanced ESS exists that is continuously stable, whereas if  $\theta < c$  the balanced ESS is not a CSS.

#### THE DISPERSAL CONFLICT

Natal dispersal, which helps to reduce sibling competition for the same resources and to avoid inbreeding, reflects an intrasibship conflict. It confers a cost on the disperser, since it may reduce its viability and possibly also its fertility, whereas the benefits are enjoyed by the dispersers and by the nondispersers as well.

Many species exhibit sexual differences in their dispersal behavior, and it is not uncommon to find cases in which only one of the sexes disperses. Thus, the dispersal conflict can be considered as an asymmetric game, with male and female as two different roles (Motro 1991).

I briefly review the assumptions and the results of that gene frequency model and add some comments pertaining to the continuous stability of the various possible ESSs. The model assumes a population of sexually reproducing haploid organisms and an environment that is divided into an infinite number of sites, each occupied by a single breeding pair, a male and a female. Generations are discrete and nonoverlapping.

Dispersal is under offspring control. Each descendant either remains at its natal site or disperses, with probabilities that are determined by its own genotype. Thus, the dispersal strategy of an individual can be represented by its genetically determined probability of choosing to disperse. Decision rules can be different

for males and for females. Progeny that leave their natal site are uniformly dispersed over the entire range of the population.

The succeeding pair of a site is chosen at random from among all pairs of young individuals present at that site. These individuals are either the undispersed descendants of the former occupants or immigrants, the descendants of pairs that occupied other sites in the preceding generation.

There is a cost associated with dispersal (denoted by  $1 - \beta$ , where  $0 \leq 1 - \beta < 1$ ), which reflects the higher mortality rate confronted by the dispersers. There is also a cost to inbreeding ( $\sigma$ ,  $0 \leq \sigma \leq 1$ ), which reflects the postulate that a pair of sibs is less likely to succeed as a breeding pair (e.g., because of infertility) than any given pair of nonsibs. (Because of the assumption of uniform dispersal, any pair is composed either of full sibs or of nonrelatives.)

It turns out (Motro 1991) that, if the cost of inbreeding is low (i.e.,  $\sigma < 1/(1 + 2\beta)$ ) if  $1 - \beta < 1/2$  or  $\sigma < 1/2(2 - \beta)/(1 + \beta)$  if  $1 - \beta \geq 1/2$ ), the only ESS is a balanced one (i.e., implying the same evolutionarily stable dispersal strategies for females as for males) and is continuously stable.

If, however, the cost of inbreeding is high but the cost of dispersal is low (i.e.,  $\sigma \geq 1/(1 + 2\beta)$  and  $1 - \beta < 1/2$ ), two more ESSs, in addition to the balanced one, exist on the boundaries of the strategy space, reflecting complete dispersal by one sex and a reduced, yet positive, dispersal strategy for the other. Both boundary ESSs are continuously stable, whereas the balanced ESS is no longer a CSS.

If the cost of inbreeding and the cost of dispersal are both high (i.e.,  $\sigma \geq 1/2(2 - \beta)/(1 + \beta)$  and  $1 - \beta \geq 1/2$ ), two boundary ESSs again exist, in addition to the balanced ESS, but here they reflect sedentariness of one sex and a positive dispersal strategy (and even complete dispersal, if  $\sigma \geq 1 - \beta$ ) for the other. It is interesting to note that, in a subset of this parameter set, two more ESSs can exist. These are inner points of the strategy space that are not on the diagonal, thus reflecting positive but different dispersal strategies for the two sexes, and are never continuously stable. Whenever they exist, the boundary ESSs and the balanced ESSs are all CSSs. (Otherwise, only the boundary ESSs, but not the balanced ESS, are continuously stable.) Hence, the existence of boundary ESSs does not rule out the possibility for continuous stability of the balanced ESS.

#### DISCUSSION

This article considers certain dynamic properties of evolutionary stability in continuous asymmetric games. Following Maynard Smith (1977) and Grafen and Sibly (1978), an ESS of an asymmetric game (or a "two types of player" game) is a pair of strategies, one for each type of player, such that, if the combined population is fixed at these strategies, no mutant of either type can be established in that population.

An important question is what happens to a population that is fixed not at an ESS but at a nearby, different strategy. Indeed, as a result of the frequent perturbations in environmental parameters, for example, any ESS population will eventually find itself in such a situation. Is then the ESS, which is a stable strategy according to the evolutionary stability criterion, also stable in a dynamic respect?

To wit, can the ESS induce an evolutionary process that will bring the population closer to it? While a similar question has already been treated for symmetric games (Eshel and Motro 1981; Eshel 1983; Taylor 1989; Christiansen 1991), the present article is a modest attempt to generalize the ideas to asymmetric games.

With this respect of dynamic stability, two different types of ESSs can be distinguished in asymmetric games: ESS that are continuously stable and ESSs that are not. A population that is fixed at any strategy in a neighborhood of a continuously stable ESS can always be invaded by mutants that are closer to the ESS. In contrast, any neighborhood of an ESS that is not continuously stable always contains a nonzero measure set of strategies that are not immune to mutants (of both types) having strategies that are further away from the ESS. Thus, in natural situations, one can expect more frequently to find populations at (or near) an ESS that is continuously stable than at (or near) an ESS that is not continuously stable.

While this article specifies certain conditions for this type of stability, the actual dynamic process that presumably carries the population toward convergence to the continuously stable ESS has yet to be studied.

The above-mentioned definition of an asymmetric ESS tacitly excludes the possibility of a "double-mutant" appearance. Certainly, this restriction is an appropriate assumption in many asymmetric games, in which the genetic systems that determine the strategies of the different types operate independently in each role (this was the assumption in the models of male-female conflicts presented here). However, in many cases, a single mutation can affect the strategies of both roles, and a different definition of evolutionary stability, such as that suggested by Taylor (1979), should be considered. In such cases, the notion of continuous stability should be redefined.

#### ACKNOWLEDGMENTS

I thank P. Taylor and M. Uyenoyama for important comments and suggestions.

#### APPENDIX

##### GENERAL EXPECTED PROGENY SIZE (EPS) FUNCTION

Let the expected progeny size  $F(z)$  (where  $z = x + y + \theta xy$  is the effective parental investment) be any increasing and concave function of  $z$ , with  $F(0) = 0$ . Thus  $R$  (in eq. [3]) is  $F(z')/F(z)$ , where  $z' = x' + y + \theta x'y$ .

The equation  $\partial W_F(x', x, y)/\partial x'|_{x'=x} = 0$  yields

$$(\theta y + 1)(cx + 1)G(z) - cF(z) = 0, \quad (\text{A1})$$

where  $G(z) = dF(z)/dz$ . Balanced ESSs are obtained by setting  $x = y$  in equation (A1), which gives

$$(\theta y + 1)(cy + 1)G(2y + \theta y^2) - cF(2y + \theta y^2) = 0 \quad (\text{A2})$$

(where the asterisks have been omitted for simplicity). Note that, for  $y = 0$ , the function in the left-hand side of equation (A2) is positive. The derivative (with respect to  $y$ ) of that function is  $(\theta - c)G(2y + \theta y^2) + 2(\theta y + 1)(cy + 1)H(2y + \theta y^2)$ , where  $H(z) = d^2F(z)/dz^2$ .

By differentiating equation (A1) with respect to  $y$  and putting  $x = y = y^*$ , we get

$$1 + \left. \frac{d\hat{x}(y)}{dy} \right|_{y=y^*} = \frac{(\theta - c)G(2y + \theta y^2)}{(\theta y + 1)^2(cy + 1)H(2y + \theta y^2)} \Big|_{y=y^*} \quad (\text{A3})$$

If  $\theta > c$ , equation (A3) implies that  $d\hat{x}(y)/dy|_{y=y^*} > -1$ . If equation (A2) does not have a solution, the only balanced ESS is  $(x^*, y^*) = (1, 1)$  and it is continuously stable. Otherwise, there exists a balanced ESS, where the derivative of the left-hand side of equation (A2) is negative. At this point, the right-hand side of equation (A3) is smaller than two, thus  $d\hat{x}(y)/dy|_{y=y^*} < 1$ . Hence inequality (1) is satisfied, and the balanced ESS is continuously stable.

If  $\theta < c$ , equation (A3) then implies  $d\hat{x}(y)/dy|_{y=y^*} < -1$ . Hence inequality (1) is not satisfied, and any balanced ESS different from  $(1, 1)$  is not continuously stable.

## LITERATURE CITED

- Christiansen, F. B. 1991. On conditions for evolutionary stability for a continuously varying character. *American Naturalist* 138:37–50.
- Eshel, I. 1983. Evolutionary and continuous stability. *Journal of Theoretical Biology* 103:99–111.
- Eshel, I., and M. W. Feldman. 1991. The handicap principle in parent-offspring conflict: comparison of optimality and population-genetic analyses. *American Naturalist* 137:167–185.
- Eshel, I., and U. Motro. 1981. Kin selection and strong evolutionary stability of mutual help. *Theoretical Population Biology* 19:420–433.
- Eshel, I., and E. Sansone. 1991. Parent-offspring conflict over the sex ratio in a diploid population with different investment in male and in female offspring. *American Naturalist* 138:954–972.
- Gaunersdorfer, A., J. Hofbauer, and K. Sigmund. 1991. On the dynamics of asymmetric games. *Theoretical Population Biology* 39:345–357.
- Grafen, A., and R. Sibly. 1978. A model of mate desertion. *Animal Behaviour* 26:645–652.
- Hammerstein, P. 1981. The role of asymmetries in animal conflicts. *Animal Behaviour* 29:193–205.
- Hammerstein, P., and G. A. Parker. 1982. The asymmetric war of attrition. *Journal of Theoretical Biology* 96:647–682.
- Matessi, C., and I. Eshel. 1992. Sex ratio in the social Hymenoptera: a population-genetics study of long-term evolution. *American Naturalist* 139:276–312.
- Maynard Smith, J. 1977. Parental investment: a prospective analysis. *Animal Behaviour* 25:1–9.
- . 1982. *Evolution and the theory of games*. Cambridge University Press, Cambridge.
- Maynard Smith, J., and G. A. Parker. 1976. The logic of asymmetric contests. *Animal Behaviour* 24:159–175.
- Motro, U. 1988. Evolutionarily stable strategies of mutual help between relatives having unequal fertilities. *Journal of Theoretical Biology* 135:31–39.
- . 1989. Should a parasite expose itself? (some theoretical aspects of begging and vigilance behavior). *Journal of Theoretical Biology* 140:279–287.
- . 1991. Avoiding inbreeding and sibling competition: the evolution of sexual dimorphism for dispersal. *American Naturalist* 137:108–115.
- Selten, R. 1980. A note on evolutionarily stable strategies in asymmetric animal conflicts. *Journal of Theoretical Biology* 84:93–101.
- Taylor, P. 1979. Evolutionarily stable strategies with two types of player. *Journal of Applied Probability* 16:76–83.
- . 1989. Evolutionary stability in one-parameter models under weak selection. *Theoretical Population Biology* 36:125–143.

*Associate Editor: Marcy Uyenoyama*