

Infanticide as an evolutionarily stable strategy

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Abstract. An evolutionarily stable strategies analysis of infanticide, expressed as two pure strategies, shows that the equilibrium frequency of infanticide depends on only two parameters: the relative advantage of infanticide when others are also infanticidal and the relative advantage of a non-infanticidal strategy if others are non-infanticidal. The possible equilibrium conditions of strictly infanticidal, strictly non-infanticidal, stably polymorphic or history-dependent populations correspond to various earlier models of infanticide. Thus, these earlier models may be subsumed as special cases of the ESS analysis. This permits the comparison of alternative theories of infanticide in specific cases of infanticide in natural populations. In particular, it is argued that if infanticide confers a relative advantage on the perpetrator when other population members are non-infanticidal, this is sufficient to reject a 'maladaptive' explanation for infanticide. The potential existence of history-dependent equilibria suggests there will be extreme difficulty with non-experimental methods that attempt to test the adaptiveness of infanticidal behaviour.

Infanticide—the killing of pre-reproductive individuals by conspecifics—is widespread among both vertebrates and invertebrates (Fox 1975; Polis 1981). Recent discussions of infanticide have focused on its selective advantages and disadvantages (Angst & Thommen 1977; Hrdy 1977, 1979; O'Connor 1978; Rohwer 1978; Sherman 1981). Most of this work has implicitly assumed that the selective advantage of infanticide is constant. In many circumstances, this is probably not a reasonable assumption. An infanticidal individual may have its reproductive advantage (cf. Hrdy 1979) progressively diminished as the frequency of infanticide increases in the population, if engaging in infanticide exposes its own offspring to increased mortality risks from other infanticidal animals. If this cost is sufficiently large, infanticide might actually be less advantageous than a non-infanticidal strategy when infanticide is widespread. This could lead to a behavioural polymorphism, or a mixed evolutionarily stable strategy (ESS), in the population (Maynard Smith 1982).

Chapman & Hausfater (1979) observed this shift in relative fitness during their simulations of langur (*Presbytis*) population dynamics as affected by infanticide. Infanticidal langurs always had a reproductive advantage in non-infanticidal populations but were at a disadvantage in some infanticidal populations, because more of their offspring

were killed than were those of non-infanticidal individuals. Stinson (1979) also found frequency effects on fitness in his simulations of fratricide in raptor populations. However, in this case, the fitness of infanticidal individuals was positively correlated to its frequency in the population.

These simulation studies indicate that the relative fitness of infanticidal behaviour is likely to be influenced by the population composition. When this is the case, attempts to predict the behavioural characteristics of populations by maximizing average fitness can produce misleading results. When selection is frequency-dependent, evolution need not maximize mean individual fitness (Maynard Smith 1974; Auslander et al. 1978). This suggests that optimization techniques are not likely to be useful in determining the equilibrium frequency of infanticide in a population.

Game theory has been used successfully in the analysis of animal conflict (see Maynard Smith 1982) where the fitnesses of alternative strategies (behavioural phenotypes) are dependent upon the frequency of the strategies in the population. However, Polis (1981) has questioned whether game theory can be applied to understanding intraspecific predation (including infanticide).

In this paper we show that game theory can be usefully applied to the study of infanticide. An ESS analysis of a simple game-theoretic model demonstrates that previous models of infanticide (Christian 1978; Curtin & Dolhinow 1978; Chapman & Hausfater 1979; Hrdy 1979; Stinson 1979) can be

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unified. Re-examining the theories in this light shows that, from an evolutionary perspective, they differ only in the values of two parameters. These parameters provide simple criteria to predict when populations at evolutionary equilibrium will be strictly infanticidal, strictly non-infanticidal, or polymorphic.

THE MODEL

Consider a large population made up almost entirely of individuals which are non-infanticidal a fraction P of the time. By this, we mean a potential perpetrator leaves an infant unharmed with probability P . This probability is a summary variable for the many underlying behavioural processes that may impinge on the outcome of such an encounter. If there are a few individuals in the population who use a different strategy and are non-infanticidal with probability P' ($P' \neq P$), we wish to know if strategy P will persist through time or if strategy P' will increase in frequency and tend to eliminate P . According to evolutionarily stable strategy analysis (Maynard Smith 1982), individuals using P' remain rare if a population exhibiting P resists invasion by individuals using strategy P' if

$$W_P(P) > W_P(P') \quad (1a)$$

or

$$W_P(P) > W_{P'}(P') \text{ when } W_P(P) = W_{P'}(P') \quad (1b)$$

Here, $W_P(P)$ is the fitness of individuals using strategy P in a population of individuals using P , and $W_{P'}(P')$ is the corresponding fitness of individuals using strategy P' . When these inequalities hold, individuals who are non-infanticidal with a frequency of P' never increase in relative frequency through selection. Thus the strategy P is evolutionarily stable (Maynard Smith 1974, 1982).

To apply these abstract conditions to the evolution of particular behavioural phenotypes, we must specify the possible strategies and the relationship between the phenotypes and their fitnesses. Suppose there are only two pure strategies. Assume that individuals encountering potential victims kill them or do not, independently of whether their own offspring are killed. A strictly non-infanticidal individual that encounters only other non-infanticidal individuals has a reproductive success of N , while strictly infanticidal individuals have a reproductive success of I . Various studies (Hrdy 1979;

Polis 1981) indicate that infanticidal and non-infanticidal individuals differ in their reproductive success: hence N and I are likely to be unequal. Suppose non-infanticidal individuals can expect to lose a portion $(1-Q)$ of their offspring to infanticide, so their reproductive success is reduced to QN ($0 < Q < 1$). Similarly, infanticidal individuals can expect to have their reproductive success reduced to $Q'I$ by other infanticidal individuals. If interactions are pairwise, these parameters are sufficient to specify all possible ESSs (Auslander et al. 1978; Maynard Smith 1982). The ESSs depend only on the difference between $Q'I$ and QN , and the difference between N and I . Let Δ_1 be $(Q'I - QN)$ and Δ_2 be $(N - I)$. The quantity Δ_1 is the relative advantage of being infanticidal when others are infanticidal, and Δ_2 is the relative advantage of being non-infanticidal when others are non-infanticidal.

In the special case that individuals interact randomly, explicit expressions can be derived for (1a) and (1b) in terms of Δ_1 and Δ_2 . Under this assumption, individuals who use the common strategy P when interacting among themselves, have fitness

$$W_P(P) = P^2(\Delta_1 + \Delta_2) - P(\Delta_1 + Q'I - I) + Q'I \quad (2a)$$

Similarly, rare individuals who are non-infanticidal with probability P' have a fitness of

$$W_{P'}(P') = P'P(\Delta_1 + \Delta_2) - P'(\Delta_1) + P(1 - Q')I + Q'I \quad (2b)$$

Note that the rare phenotype's fitness is a linear function of the frequency of non-infanticidal behaviour used by the common phenotype (2b). If the rare phenotype is strictly non-infanticidal ($P' = 1$) its fitness is described by the graph of the straight line

$$W_{P'}(P' = 1) = P(1 - Q)N + QN \quad (3a)$$

with end-points QN and N when the common strategy is either strictly infanticidal or strictly non-infanticidal, respectively. If the rare phenotype is strictly infanticidal, its fitness is described by

$$W_{P'}(P' = 0) = P(1 - Q')I + Q'I \quad (3b)$$

with end-points $Q'I$ and I . Δ_1 and Δ_2 represent the difference in fitness for the two rare strategies when the common strategy is either strictly infanticidal (Δ_1) or strictly non-infanticidal (Δ_2) (Fig. 1).

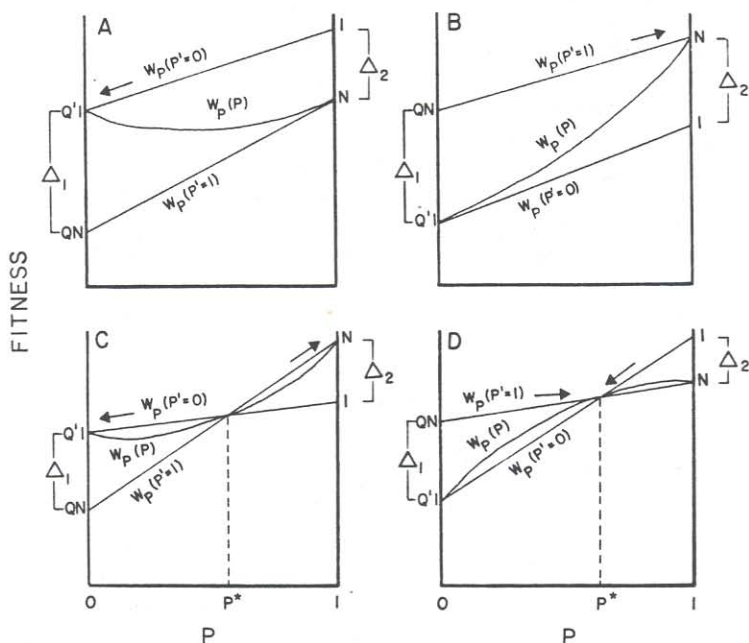


Figure 1. Four possible evolutionary solutions when infanticidal behaviour is determined by frequency-dependent selection. Infanticide may be: fixed (A), eliminated (B), fixed or eliminated, depending upon the population's history (C), or maintained at intermediate frequencies (D). The horizontal axis is the frequency of infanticide used by individuals with the common strategy. $W_P(P'=0)$ and $W_P(P'=1)$ represent the fitnesses of strictly infanticidal and strictly non-infanticidal rare mutants when the common strategy is P . Δ_1 and Δ_2 are the differences in fitnesses for these strategies when the common strategy is strictly infanticidal (Δ_1) and strictly non-infanticidal (Δ_2). $W_P(P)$ is the fitness of individuals using the common strategy as P varies. Arrows indicate the direction of evolution in the frequency of non-infanticidal behaviour towards an ESS.

Simple algebra shows that the fitness of any rare mixed strategy ($0 < P' < 1$) is described by the straight line (2b) and is bounded by the lines (3a) and (3b). To determine the ESS, compare the fitnesses of rare phenotypes with the fitness of the common strategy (1a and 1b). The fitness of the common strategy (2a) is a quadratic function of P and is bounded by $W_P(P'=0)$ and $W_P(P'=1)$, taking values of $Q'1$ when $P=0$ and N when $P=1$. There are four possible scenarios to consider (Fig. 1A–D). In the first case (Fig. 1A) the rare infanticidal phenotype is always more fit than the rare non-infanticidal phenotype, regardless of the strategy used by the remainder of the population ($\Delta_1 > 0$ and $\Delta_2 < 0$). As a result, the rare infanticidal individual also does better than any other rare strategy and, because it lies above the graph of the common phenotype's fitness, for all values of $P > 0$ it has a selective advantage and is able to increase. Thus, the only ESS is one that is strictly infanticidal.

By a similar argument, when a strictly non-infanticidal strategy is the best rare strategy ($\Delta_1 < 0$ and $\Delta_2 > 0$) its fitness exceeds any other common strategy (Fig. 1B) and it is able to invade. Thus, the only ESS is a strictly non-infanticidal strategy.

If infanticide has a relative advantage when others are infanticidal ($\Delta_1 > 0$) but a non-infanticidal strategy has an advantage when others are non-infanticidal ($\Delta_2 > 0$), the graphs of the fitnesses of the rare phenotypes and the common phenotype cross (Fig. 1C) at some intermediate frequency of P which is determined by $P^* = \Delta_1 / (\Delta_1 + \Delta_2)$.

At the intersection of these curves all rare strategies and the common strategy have the same fitness and are at equilibrium. However, the equilibrium is unstable because any perturbation in P away from P^* towards more frequent non-infanticidal strategies gives rare non-infanticidal phenotypes a greater fitness than the common form. Similarly, perturbations of the equilibrium towards more infanticidal strategies gives rare infanticidal

mutants greater fitness than the common form. Under these conditions strictly infanticidal or strictly non-infanticidal strategies represent alternative ESSs. The one that occurs in any particular situation will depend on P^* and the direction of the perturbation away from P^* .

The final case occurs when a non-infanticidal strategy is the best strategy against an infanticidal strategy ($\Delta_1 < 0$), while an infanticidal strategy has a greater fitness against a non-infanticidal strategy ($\Delta_2 < 0$). As before, the graphs of the fitnesses for the various strategies intersect at an intermediate value of P (Fig. 1D). However, in this situation if the common strategy is exposed to a more non-infanticidal rare strategy its fitness is greater; the rare phenotype cannot increase and if it is exposed to a more infanticidal rare strategy the common phenotype's fitness is greater so the rare phenotype, again, cannot invade. Thus, the intermediate strategy continues to persist as a mixed ESS.

In short, given two strategies competing against each other, we might observe unilateral selection towards one or the other pure strategies, a stable mixture, or a situation in which the initial conditions determine the equilibrium structure of the population.

DISCUSSION

Infanticide is a topic that has engendered much debate (e.g. Dolhinow 1977; Hrdy 1977, 1979; Curtin & Dolhinow 1978; Polis 1981; Sherman 1981), and most of the disagreement seems to concern the paradigm that should be used to interpret infanticide (viz. a maladaptive stress response versus an adaptive reproductive strategy). It has been difficult to determine how these views actually differ from one another in their predictions, which has created problems for determining which view should be applied to particular cases of infanticide. Our ESS analysis provides criteria to distinguish between previous models of infanticide on the basis of the parameters Δ_1 and Δ_2 . As such, it subsumes these earlier attempts as special cases of the ESS model.

'Maladaptive' models of infanticide (Dolhinow 1977; Curtin & Dolhinow 1978), such as the social stress hypothesis, contend that infanticide is not adaptive, but rather results from physiological and behavioural responses to the environment (Christian 1978, 1980). By definition, these models

require that infanticide should not confer a reproductive advantage on the perpetrator. In terms of our model, they limit the possible selective regimes to cases where $\Delta_1 < 0$ and $\Delta_2 > 0$ (Fig. 1B). Therefore, the critical test of maladaptive theories, in specific cases of infanticide, can be determined by examining the relative advantage of infanticide when others are non-infanticidal (Δ_2). In particular, Δ_2 should never be negative (infanticide has a relative advantage) if maladaptive theories are correct.

Several experimental studies have examined the reproductive success of infanticidal individuals when infanticide by other population members was reduced or eliminated, and they have found that infanticidal individuals did have a higher reproductive success ($\Delta_2 < 0$). For example, laughing gulls (*Larus atricilla*) fledge more chicks when brood reduction is permitted than when it is prevented (Hahn 1981). Female mountain dusky salamanders (*Desmognathus ochrophaeus*) are reproductively more successful if they are infanticidal (Forester 1979), and infanticidal male *Mus musculus* and *Dicrostonyx groenlandicus* breed more rapidly than non-infanticidal conspecifics (Mallory & Brooks 1978; vom Saal & Howard 1982). Several other studies show that infanticide is correlated with improved juvenile survival rates (LeBeouf et al. 1972; Howe 1976, 1978; Reiter et al. 1981). In each of these species infanticide appears to provide a direct benefit to the perpetrator. This seems to falsify maladaptive models in these cases.

Most adaptive models of infanticide have emphasized factors favouring the maintenance of infanticidal traits (Fox 1975; Rohwer 1978; Hrdy 1979; Polis 1981). These discussions have tended to ignore the possibility that infanticide may result in frequency-dependent selection. If fitnesses are constant, in our model, one or the other pure strategies must become fixed in the population and any polymorphism must be transient (Fig. 1A, B). However, stable infanticidal polymorphisms seem to occur in a number of vertebrates and invertebrates (Bragg 1946, 1956, 1964; Parsons 1971; Rhodes & Merriner 1973; Polis 1981) and must be accounted for by any adaptive model of infanticide. According to our analysis, stable polymorphisms should be expected if both pure strategies are disadvantageous when common (Fig. 1D).

Chapman & Hausfater (1979) were the first to suggest that infanticide might persist as a polymorphic ESS (see also Hausfater et al. 1982), and their

model has provoked interest as a way to explain the apparent differences in the frequency of infanticide observed in different langur (*Presbytis entellus*) populations (Hrady, 1979). A stable polymorphism occurs because infanticidal individuals have a relative advantage in populations of non-infanticidals ($\Delta_2 < 0$), but a greater proportion of their offspring are at risk in populations of infanticidals ($\Delta_1 < 0$). According to their model, infanticide might be stably polymorphic in these populations, with frequencies varying from 3% to 95%. However, their model has some limitations because, contrary to Hrady's (1979) suggestion, it predicts that strictly non-infanticidal populations can never exist. Yet such populations have been reported (Curtin & Dolhinow 1978).

Three hypotheses might be advanced to explain this apparent contradiction. First, if infanticide occurs at low frequencies it may take thousands of observer-hours before it is witnessed, and cases of 'non-infanticidal populations' may merely represent under-observed populations. For example, Armitage and his co-workers have spent extensive periods observing populations of *Marmota flaviventris* over 22 years, and in that time have seen only two cases of infanticide (Armitage et al. 1979). Alternatively, both Chapman & Hausfater (1979) and this ESS analysis assume very large populations. It might be that non-selective factors (e.g. genetic drift) could alter a population with a low equilibrium frequency of infanticide to a strictly non-infanticidal one.

A third possibility can be traced to Chapman & Hausfater's (1979) initial assumption that infanticide is always advantageous in non-infanticidal populations ($\Delta_2 < 0$). This restricts the equilibrium populations to either purely infanticidal (Fig. 1A) or polymorphic (Fig. 1D) states. If infanticide were somehow disadvantageous in non-infanticidal populations, strictly non-infanticidal populations also might be expected (Fig. 1B). The presumption that $\Delta_2 < 0$ in their model comes from an analysis of reproductive characteristics of langur populations and is '... attributable to the fact that infanticide at the time of replacement advances the onset of the female's oestrus by some number of months' (Chapman & Hausfater 1979, page 229). However, in populations of langurs where infanticide has not been reported, the loss of offspring has little if any impact on the speed at which a female returns to oestrus (Hrady 1977, 1979). Therefore, males in these populations cannot receive this reproductive

benefit by being infanticidal, and if, as reported after some instances of infanticide, the female troop splinters (Hrady 1977), infanticidal males might be less successful than males that tolerated unrelated offspring.

Thus, equilibrium non-infanticidal populations might result from frequency-dependent selection (Fig. 1B), rather than being artifacts of inadequate sampling or small-population phenomena. Although infanticide is a dramatic phenomenon when it occurs, it should be remembered that there is an apparent lack of infanticidal strategies among males in a variety of vertebrate species. If intense sexual selection among males coupled with a flexible female reproductive response to the loss of her offspring favours the selection of infanticidal males (Hrady 1979), then the absence of a female response will eliminate this benefit for the males, making $\Delta_2 \geq 0$. Among northern elephant seals, *Miroounga angustirostris* (LeBoeuf et al. 1972; Reister et al. 1981), and a variety of ungulates (Geist 1971; Clutton-Brock 1982), sexual selection among males has been well documented. In these species, females who lose their offspring do not become sexually receptive until the following reproductive season. Yet, despite intense intrasexual competition, adult males have never been reported to be infanticidal in these species. Sherman (1981) observed similar behaviour patterns among his adult male Belding's ground squirrels (*Spermophilus beldingi*). Female ground squirrels also fail to become sexually receptive following the loss of offspring. Therefore, the selective advantage of infanticide by males often seems to depend on the prior existence of a labile reproductive response by females, which seems less likely in seasonal breeders.

Stinson (1979), in a discussion of fratricide among raptors, suggested that under certain conditions, alternative, stable equilibria might be observed, and that there were alternative selective regimes that could lead to the same equilibrium condition. He noted that non-infanticidal chicks in a nest with infanticidal siblings have a fitness close to zero because they are killed by their siblings. Infanticidal chicks under the same conditions are likely to have a greater fitness because they may kill their siblings before they are killed. Thus, according to the ESS analysis, Δ_1 is positive. Stinson also noted there were two ways that infanticide could become fixed in the population. In the first case, when an infanticidal chick's survival was suffi-

ciently large its fitness exceeded that of non-infanticidal chicks ($\Delta_2 < 0$). Infanticide became fixed in the population because it was always advantageous (Fig. 1A). Alternatively, if the frequency of infanticide was sufficiently large, initially, infanticide would become fixed even though infanticidal individuals might have a lower fitness than non-infanticidal siblings ($\Delta_2 > 0$).

In this case, both pure strategies act as a positive feedback on themselves ($\Delta_1 > 0, \Delta_2 > 0$). This corresponds to an unstable polymorphism, P^* , with strictly infanticidal or strictly non-infanticidal populations as alternative ESSs (Fig. 1C). Under these conditions, populations with identical selective regimes may reach alternative stable equilibria if the initial frequencies of infanticide differ. This clearly increases the difficulty of making claims about the adaptive significance of infanticide, because in a given physical environment and social structure infanticide may become fixed or not depending only on the population's history.

Thus, by themselves none of the previous models of infanticide are sufficient to describe the diversity of phenomena that have been reported. However, if they are considered as alternative special cases of the ESS analysis, the differences among them can be viewed as involving the choice of values for Δ_1 and Δ_2 . To apply this model to infanticide in natural populations involves determining the range of values for Δ_1 and Δ_2 that occur. To our knowledge, no studies have been performed that simultaneously evaluate both parameters. In the studies that have examined the relative success of infanticidal and non-infanticidal individuals in the same population, the results indicate that the perpetrator experiences a net benefit (see above). Because infanticide by other conspecifics was usually controlled in these studies, this is equivalent to $\Delta_2 < 0$. We are unaware of any studies, in field populations, when the perpetrator has been shown to be at a relative disadvantage. These results indicate that infanticide should be expected to persist at least as a polymorphic strategy (Fig. 1A, D) and that maladaptive and history-dependent theories are not appropriate in these situations.

Whether these populations should be polymorphic or strictly infanticidal depends on the relative advantage of infanticide when conspecifics are also infanticidal (Δ_1). Few studies have explicitly compared the reproductive success of infanticidal and non-infanticidal individuals when their offspring

are at risk from conspecifics. However, John Hoogland (personal communication) has observed several cases of infanticide among black-tailed prairie dogs (*Cynomys ludovicianus*) where females lost their litters to other infanticidal females while they were away from their burrows committing infanticide. In this case, infanticidal individuals would seem to have an additional cost associated with their strategy that non-infanticidal individuals can avoid. This cost may be widespread among species when parental defence against infanticide is a successful counter-strategy. Among many of the Laridae, parental defence effectively deters most attacks against the young by neighbours (Emlen 1956; Fordham 1970; Parsons 1971; Fetterolf 1983) and infanticide occurs if the parents are absent or the chicks are not defended. Similarly, Yom-Tov (1974) reports that the probability of crow (*Corvus corone*) eggs or chicks being destroyed increases with the length of time parents leave their nest unattended. The importance of parental guarding in protecting offspring from conspecifics also is reported in several Amphibia. Forester (1979) showed that removing adult females from their clutches frequently resulted in egg cannibalism by conspecifics, while guarding females were usually able to protect their eggs from such attacks. Kluge (1981) observed a similar pattern among nest-guarding male gladiator frogs (*Hyla rosenbergi*). These results suggest that when infanticide occurs and there are possible counter-strategies, such as parental care, non-infanticidal reproductives may be at a relative advantage ($\Delta_1 < 0$) when infanticide is common, and infanticide will persist as a polymorphic strategy.

Our analysis also has some significant implications for past attempts to examine the adaptiveness of infanticide, and it identifies an experimental approach to examine its adaptiveness in future studies. One proposed test has been to examine the relative reproductive success of individuals in infanticidal and non-infanticidal populations (Warren 1967; Bygott 1972; Curtin & Dolhinow 1978). If infanticidal populations are less productive than non-infanticidal populations, then infanticide is maladaptive. However, this is an inappropriate test because it compares $W_P(P)$ to $W_P(P')$, which are not the conditions for an ESS (1A, 1B); individual fitness must be compared within populations; and not average fitness across populations. Even though infanticide may be adaptive, mean individual fitness need not be maximized under

frequency-dependent selection (Maynard Smith 1974; Auslander et al. 1978).

A second proposal has been to conduct 'natural experiments' which compare populations living in similar environments (Warren 1967; Hrdy 1979). Attempts are then made to correlate differences in one or two environmental factors with differences in the behaviour between populations. Usually, no measures of reproductive success for alternative strategies are made. Note that if there are no estimates of Δ_1 and Δ_2 , there is no assurance that populations will not have a selective regime that produces history-dependent equilibria (Fig. 1C). Under these conditions, even if populations had identical selective regimes they could differ in their frequencies of infanticide simply by starting with different frequencies of infanticide. As discussed above, no studies have demonstrated the need to hypothesize history-dependent equilibria, but so little research has been done that such a possibility should not be dismissed. As Stinson's (1979) simulation shows, such conditions are not particularly unusual or restrictive and should not be ignored. Failing to measure reproductive success and consider history-dependent conditions in 'natural experiments' may lead to rejecting an adaptive theory of infanticide altogether, or postulating the influence of unmeasured environmental parameters. Data from comparative field studies must be interpreted cautiously.

Probably the simplest and most straightforward experimental approach to test the adaptiveness of infanticide is to compare the relative reproductive success of infanticidal and non-infanticidal individuals when infanticide by others is prevented. The actual procedures necessary to perform this depend on the particular species under study, but workers are referred to the papers discussed above for a variety of approaches. This procedure, effectively, permits one to evaluate Δ_2 . Finding that infanticidal individuals are more successful than non-infanticidal individuals ($\Delta_2 < 0$) is a sufficient condition to reject a maladaptive theory of infanticide (Fig. 1B). The test, however, is asymmetric in that if $\Delta_2 > 0$ one cannot accept a maladaptive theory for infanticide. This is because an infanticidal strategy may be at a relative disadvantage when others are non-infanticidal yet still become fixed in the population if history-dependent conditions apply (Fig. 1C, $\Delta_1 > 0$). Thus, if infanticide is shown to be disadvantageous when other sources of infanticide are prevented, it then becomes necessary

to examine how well infanticidal and non-infanticidal individuals fare when infanticide by conspecifics is common.

This restructuring of previous models of infanticide as special cases of an ESS is intended to improve the dialogue among users of competing theories by showing the communality among them. Much of the current debate seems to reflect a failure to appreciate the implications and rich evolutionary results that derive from frequency-dependent selection. Hopefully, future experimental manipulations will be aimed at measuring some of these parameters, such as Δ_2 , so that the relative significance of the alternative theories to natural populations may be evaluated.

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