Paternal Investment by Terrestrial Arthropods[1]

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Synopsis. Paternal investment in terrestrial arthropods occurs in three contexts. Pre-zygotic investment includes indirect contributions to offspring through nutrients provided to the male's mate. Biparental care refers to joint male and female care of offspring. Finally, exclusive paternal care occurs when only the male invests in offspring following oviposition. Examples of exclusive paternal care are known in insects such as assassin bugs (Reduviidae), harvestmen (Opiliones), and millipedes (Diplopoda), although it is far more common in a group of secondarily aquatic insects, namely, the giant water bugs (Belostomatidae). Biparental care is also uncommon and is best developed in burying beetles (Silphidae), dung beetles (Scarabaeidae), and termites (Isoptera). The most pervasive type of paternal investment appears to be prezygotic in the form of spermatophore products and other "nuptial gifts" provided to the female parent.

The evolution of paternal investment is a complex process and no single hypothesis nor evolutionary pathway appears adequate to explain the diversity of paternal investment strategies in terrestrial arthropods. As is the case with other animal groups, paternal investment is correlated with certainty of paternity and male territoriality. Ecological factors also appear important, especially in the way these influence the ability of males to enhance the survivorship of offspring and/or the fecundity of their mates. Physically harsh or biotically dangerous habitats and ephemeral, highly prized, productive resources are all associated with high levels of paternal investment. Finally, the indirect sperm transfer strategies common to many terrestrial arthropod species seem to preclude males from contributing materially to their offspring by dissociating parent from progeny. This dissociation may explain in part the relative paucity of high levels of paternal investment by terrestrial arthropods.

Introduction

The trade-off between enhanced offspring survival and reduced future reproduction by the parents should determine the resources organisms allocate to parental duties. This trade-off is fundamental to Trivers' (1972) concept of parental investment which Wittenberger (1981) has expanded to mean ". . . any investment in offspring by a parent that enhances the survival prospects of current offspring while reducing the parent's ability to invest in other current offspring or to produce future offspring." The benefits and costs of parental investment depend on constraints imposed by the abiotic and biotic components of the environment as well as particular attributes of the species themselves. For example, whether or not egg predators cause natural selection for parental care of eggs depends not only on the foraging strategy of the predator but also on the intrinsic ability of the parents to protect the eggs. This ability is determined by morphological and behavioral characteristics unique to each species. The costs of parental investment also tend to differ for the two sexes (Trivers, 1972). For males, parental investment is often made at the expense of attracting additional mates. For females, investment in current offspring is balanced against a reduction in the probability of obtaining sufficient energy and nutrients for future offspring. In this paper we focus our discussion on the evolution of paternal investment with particular emphasis on terrestrial arthropods.

SPERM TRANSFER
IN TERRESTRIAL ARTHROPODS

GROUP I
INDIRECT SPERMATOPHORE
TRANSFER WITH PAIR FORMATION

Male deposits spermatophore on
substrate while enticing a particular
female to pick it up.

Arachnids:
  mites (some)
  pseudoscorpions (some)
  schizomids
  scorpions
  tailless whipscorpions
  whipscorpions
Insects:
  collembolans (some)
  thysanurans
Other:
  centipedes (some)
  millipedes (some)
  onychophorans (some)

GROUP II
INDIRECT SPERMATOPHORE
TRANSFER WITHOUT PAIR FORMATION

Male deposits spermatophore on
substrate and departs; female secures
it unassisted.

Arachnids:
  mites (some)
  pseudoscorpions (some)
Insects:
  collembolans (some)
  diplurans
Other:
  millipedes (some)
  pauropods
  symphylans

GROUP III
DIRECT SPERM(ATOPHORE)
TRANSFER

Male transfers sperm or spermato-
phore to female's genital aperture.

Arachnids:
  harvestmen
  mites (some)
  ricinuleids
  spiders
  solpugids
  ticks
Insects:
  all pterygotes
Other:
  centipedes (some)
  isopods
  millipedes (some)
  onychophorans (some)

Fig. 1. An evolutionary sequence for the development of sperm transfer mechanisms in terrestrial arthropods. Alexander (1964) was the first to propose this sequence.

Most animal species are, in fact, terrestrial arthropods. This grouping includes the vast majority of insects, arachnids, myriapods, onychophorans and a minority of the isopod crustaceans. The diversity of reproductive, life history, and parental investment strategies in this group is unparalleled in the animal kingdom. Mating behavior and methods of sperm transfer range from male deposition of sper- matophores on the substrate irrespective of the presence of females to insemination with liquid sperm using copulatory organs (Fig. 1; Alexander, 1964; Schaller, 1971; Thomas and Zeh, 1984). Similarly, paternal investment strategies are highly variable. Although most terrestrial arthropod species provide no paternal (or maternal) care, in some species one or both of the parents assiduously nurture the offspring

through several nymphal or larval stages. We propose that the type of sperm transfer has important implications for paternal investment and male life histories in general (see Thomas and Zeh, 1984). This argument is developed in a later section.

Our presentation is structured as follows. First, we discuss some current hypotheses which attempt to explain why paternal investment is so rare relative to maternal investment. Then we present a modification of the game theory model for the evolution of parental care, originally proposed by Maynard Smith (1977). The model is used to clarify the role of certainty of paternity in the evolution of paternal investment, and more generally as a heuristic tool for summarizing the important variables in parental investment evolution. Then we discuss how the model relates to terrestrial arthropods. Finally, we provide a synopsis of paternal investment by terrestrial arthropods. The review considers three categories of paternal investment: prezygotic investment including indirect contributions to offspring through nutrients provided to the male's mate; biparental care involving joint male and female care of offspring; exclusive paternal care which occurs when only the male invests in offspring following egg release by the female.

EVOLUTION OF PATERNAL INVESTMENT: HYPOTHESES

Evolutionary biologists seek to identify the ultimate causes underlying variability within and between species. A most striking pattern is the differing contributions males and females make to their offspring. Where parental care does occur in terrestrial invertebrates it is generally performed exclusively by the female. Biparental care is much more common in terrestrial vertebrates but, again, it is the female which typically provides in cases of uniparental care. Teleost fishes provide a glaring counter example to female dominated parental care. Exclusive male care occurs in 50% of the families which exhibit some type of parental care (Ridley, 1978). One of the most obvious differences between aquatic and terrestrial groups is the way in

which eggs are fertilized. Because gametes rapidly desiccate in air, internal fertilization is a prerequisite for a truly terrestrial existence. By contrast, many aquatic species, including the vast majority of teleost fishes, exhibit external fertilization. Three hypotheses have been formulated to explain the association between type of parental care and the mode of fertilization. The first argues that a male should care for offspring only when his certainty of paternity is high, i.e., when he actually fertilizes a large proportion of a given mate's eggs (Trivers, 1972; Ridley, 1978; Blumer, 1979; Peronne and Zaret, 1979). External fertilization permits high certainty of paternity since eggs are fertilized in the male's presence. Paternity is less certain with internal fertilization because females may receive multiple inseminations prior to egg deposition. Overall then, given the generally higher level of female certainty of parentage, this hypothesis would predict a predominance of maternal care. A problem, however, arises in testing the certainty of paternity hypothesis since several alternative explanations predict a similar correlation between parental care and mode of fertilization (Gross and Shine, 1981; Wittenberger, 1981). Furthermore, the logic of this intuitively appealing argument is flawed (Maynard Smith, 1978; Grafen, 1980; Werren et al., 1980). Certainty of paternity cannot directly affect paternal care evolution when a male cannot increase his paternal confidence by adopting a caring role (Wittenberger, 1981). The certainty of paternity hypothesis, as presented above, is incomplete. A more logically consistent role of paternal certainty in the evolution of parental investment will be presented in the model below.

A second hypothesis also predicts a bias toward maternal care in internally fertilizing species and toward paternal care in species with external fertilization. Consider a situation in which parental care is critical to offspring survival but can be provided by a single parent nearly as effectively as by both. In such a case, both male and female should attempt to desert first, leaving the offspring with the partner (Dawkins and Carlisle, 1976; Maynard

Smith, 1977; Grafen and Sibley, 1978; Carlisle, 1981). The abandoned parent is then placed in a "cruel bind" (Trivers, 1972) in which further desertion is not advantageous. Dawkins and Carlisle (1976) point out that internal fertilization invariably leaves the female in possession of zygotes so that the male has the first opportunity to desert. They further argue that in externally fertilizing species, males have more to lose from releasing gametes first and deserting since sperm diffuse more rapidly in water than do eggs, and females typically have no difficulty in locating other males willing to fertilize their ova (Carlisle, 1981). This latter proposition assumes that most males in the population are willing to delay sperm release until after females spawn.

Although internal fertilization clearly predisposes the male to desert first, the assertion that external fertilization results in the opposite effect seems tenuous. In fact, comparative data on teleosts indicate that gamete release is often simultaneous in species with external fertilization (Loiselle, 1978). In this situation the "order of gamete release" hypothesis predicts an equal frequency of male and female uniparental care. This prediction is not realized: exclusive paternal care occurs in a majority (36/46) of species with simultaneous gamete release and uniparental care (Gross and Shine, 1981). The gamete order argument has attracted considerable attention because it offers a compellingly simple explanation for large-scale differences in the type of parental care (Carlisle, 1981). However, like the certainty of paternity hypothesis this argument is incomplete. In its strictest interpretation, the order of gamete release hypothesis could not, for example, explain parental investment differences in a group of species with the same mode of fertilization.

A third hypothesis posits unequal payoffs to parental care for the two sexes because one sex is more likely to be physically associated with the offspring than the other (Williams, 1975; Gross and Shine, 1981). Internal fertilization and delayed oviposition preadapt the female for parental care. Under these circumstances the male would

incur time costs and might forfeit additional matings simply to gain the opportunity to provide care. By contrast, the cost of male parental care is minimized when females spawn on the male's territory. This condition is typical of externally fertilizing fishes exhibiting paternal care (Ridley, 1978; Blumer, 1979; Gross and Shine, 1981). Of the three hypotheses discussed, the "association" hypothesis is most consistent with the available information on fertilization mode and type of parental care (Gross and Shine, 1981). More importantly for terrestrial arthropods, this hypothesis can explain paternal care differences in a group sharing a common mode of fertilization.

EVOLUTION OF PATERNAL INVESTMENT: GAME THEORY MODEL

The optimal level of paternal investment depends on the simultaneous effects of many variables. The restrictive hypotheses presented thus far can at best provide partial explanations of paternal care evolution. In an attempt to rectify this situation, we now present a modification of Maynard Smith's (1977) game theory model of parental care. There are three major advantages to this approach. Most importantly, the mathematical formulation allows a determination of the net effects of several competing processes. Furthermore, an evolutionary game theory approach is appropriate when fitnesses are frequency dependent (Maynard Smith, 1982), *i.e.*, when the fitness of a strategy depends not only on the rigors of the physical environment but also on the strategies adopted by other members of the population. Two possible strategies—care and desertion—are considered in the model. The fitness of each strategy in a particular sex depends on the strategy adopted by the majority of individuals in the other sex. In other words, frequency dependence arises from interactions between the sexes. The model does not incorporate within-sex frequency dependence. It assumes the fitness of a strategy to be independent of the strategies adopted by other members of the same sex. We believe that between-sex frequency dependence captures the essence of the
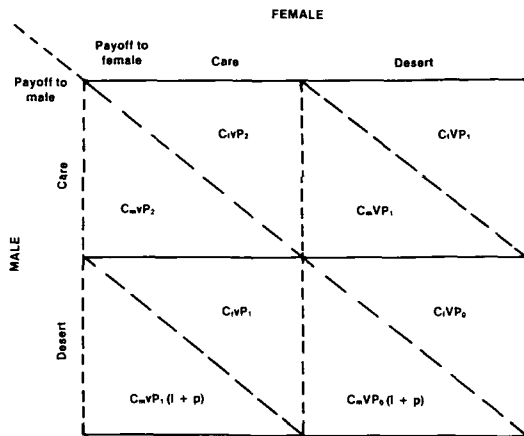
FIG. 2. Returns to male and female parents adopting caring and deserting strategies. Payoff to males are given to the left of the diagonal, while female payoffs appear on the right (modified from Maynard Smith, 1977). Symbols are as follows: 1. P_0, P_1, P_2 are the survival probabilities of offspring which are deserted by both parents, cared for by one parent, and by two parents, respectively; 2. p is the probability that a deserting male remates; 3. V, v are the number of offspring produced by deserting and caring females, respectively; 4. C_m, C_f are the certainty of parentage coefficients for males and females, respectively.

problem of paternal care evolution. More elaborate models (*e.g.*, Grafen and Sibley, 1978) have been developed which incorporate refinements such as sexual differences in parental care ability, within-sex frequency dependence, and continuous strategy sets, *i.e.*, parents that can provide care for a variable length of time. We deliberately chose to present the simpler, more intuitive model since our primary purpose is to provide an organized framework for discussing paternal care in terrestrial arthropods.

A parental care payoff matrix is presented in Figure 2. The following relations are considered. Offspring survival (P) is a function of the number of parents (0, 1, or 2) providing care. For females, the parental care trade-off between enhanced offspring survival and reduced future reproduction stems from the following: Deserting females produce more, or at least as many offspring as do caring females (V ≥ v) since the provision of care depletes resources that could otherwise be allocated to egg production (Maynard Smith, 1982).

For males, those providing care mate only once, while deserting males have some chance (p) of remating. In terms of whether natural selection favors male care, this approximates the less restrictive assumption that deserting males have a higher (or equal if p = 0) probability of finding an additional mate. Finally, the male and female payoffs are discounted by the certainty of parentage factors, C_m and C_f, respectively. This modification of Maynard Smith's original model and many of the conclusions regarding the role of parental certainty are from C. W. Petersen (unpublished manuscript).

Table 1 gives the four possible evolutionarily stable strategies (ESSs), the conditions necessary for each to be an ESS, and examples of terrestrial arthropods for each. In the model an ESS represents a pair of strategies such that:

1. if most males adopt a stragety, I_m, it would not benefit a female to adopt other than I_f and

2. if most females adopt I_f, it would not benefit a male to do other than I_m (Maynard Smith, 1977).

Certainty of paternity and the evolution of paternal care

An immediately apparent result (Table 1) is that the certainty of parentage factors, C_m and C_f, do not weigh in any of the ESS criteria. This is because C_m and C_f are assumed to be the same for caring and deserting individuals and therefore their effects cancel. For example, consider the inequality which determines if males should care given that females do:

$$C_m v P_2 > C_m v P_1 (1 + p) \qquad (1)$$

which simplifies to:

$$P_2 > P_1 (1 + p). \qquad (1a)$$

Likewise, the inequality which determines if females should care given that males do:

$$C_f v P_2 > C_f V P_1 \qquad (2)$$

simplifies to:

$$v P_2 > V P_1. \qquad (2a)$$

This analysis clarifies the role of certainty of parentage in parental care evo-

Table 1. *Evolutionarily stable parental care strategies and conditions required for their maintenance (modified from Maynard Smith, 1977).*[*]

Evolutionarily stable strategy (ESS)	Requirement for maintenance of the ESS	
	For females	For males
ESS 1: Both desert	$VP_0 > vP_1$, or female cares	$P_0(1 + p) > P_1$, or male cares
Most common ESS for terrestrial arthropods	Increased egg production exceeds benefit of uniparental care	Potential for additional mating outweighs benefit of uniparental care
ESS 2: Male D, female C	$vP_1 > VP_0$, or female deserts	$P_1(1 + p) > P_2$, or male cares
Next most common ESS for terrestrial arthropods; many Hemiptera, Homoptera, Arachnida etc.	Benefit of uniparental care exceeds increased egg production	Potential for additional mating outweighs benefit of biparental care
ESS 3: Both care	$vP_2 > VP_1$, or female deserts	$P_2 > P_1(1 + p)$, or male deserts
Found in species which must rapidly appropriate a resource for young; many dung beetles, termites, burying beetles	Benefit of biparental care exceeds loss in egg production	Benefit of biparental care outweighs potential for additional mating
ESS 4: Male C, female D	$VP_1 > vP_2$, or female cares	$P_1 > P_0(1 + p)$, or male deserts
An extremely rare ESS for terrestrial arthropods; some giant water bugs, one harvestman; some assassin bugs	Increased egg production exceeds benefit of biparental care	Benefit of uniparental care outweighs potential for additional mating

[*] Symbols are defined in Fig. 2.

lution. If parental certainty does not vary between strategies within a sex, it can have no *direct* effect on selection for care or desertion. This conclusion applies regardless of the relative value of paternal and maternal certainty.

Maynard Smith (1982) has suggested how certainty of paternity can *indirectly* affect the distribution of paternal care among species. He argues that, across species, certainty of paternity is inversely related to the chance of a second mating (p). The model therefore predicts that species with a high probability of additional matings (and low C_m) will show male desertion. Conversely, males should tend to care in species where the opportunity to remate is low (and C_m is high).

Paternal certainty directly affects parental care decisions when it is different for caring and deserting males (Wittenberger, 1981). If a male increases his certainty of paternity by providing care, then C_m no longer cancels in the inequalities which determine the stability of each ESS. To see this, consider a modification of equation 1 in which C_{mc} and C_{md} are the paternal cer-

tainties of caring and deserting males respectively. Equation 1 then becomes:

$$(C_{mc}/C_{md})P_2 > P_1(1 + p). \qquad (1b)$$

To state this relationship in words, the increase in the likelihood that males provide care is equal to the proportional increase in the paternal certainty of caring males.

Can a male's certainty of paternity increase as an immediate consequence of caring? Without explicit justification, Wittenberger (1981) asserts that paternal certainty differences between caring and deserting males arise after paternal care has already evolved. However, there are arthropod examples which strongly suggest that male parental care can be accompanied by a concomitant increase in paternal certainty. Consider, for example, alternative male strategies in sphecid wasps (see Alcock, 1975; Peckham, 1977; Coville and Coville, 1980; Hook and Matthews, 1980). Although the details vary among species and genera, the following scenario is rather typical. Females excavate nests where they oviposit and provision the lar-

vae with arthropod prey. A "guarding male" defends a nest site against conspecific males and incidentally provides paternal care by blocking the entrance of larval parasites into the nest. Because of the necessity to remain associated with a particular nest site, guarders are constrained to copulate with a small number of females. However, a guarding male copulates with a female using his territory nearly every time she returns to the nest. By contrast, males adopting a "patrolling" or "intercepting" strategy attempt to copulate with any female encountered outside the domain of a territorial male. A patroller's success rate per copulation attempt is relatively low and he must contribute only a small proportion of all the sperm received by any one of his mates. It seems clear that by guarding, a male immediately effects an increase in his certainty of paternity.

Increased certainty of paternity arising as an instantaneous consequence of paternal investment increases the payoff to investing males (see equation 1b). How pervasive is this effect? As was developed in the preceding paragraph, different levels of paternal certainty for investing and deserting males can occur when males invest postzygotically in offspring, i.e., when they provide care. However, the link between care and paternity seems to require such specific ecological conditions (e.g., male territoriality) that it is of limited general significance. By contrast, we argue that the increased certainty of paternity to be gained from prezygotic investment has broad based evolutionary significance in terrestrial arthropods. Such prezygotic investment can enhance certainty of paternity by reducing the probability and/or number of additional matings by a male's mate, or by increasing the number of sperm actually transferred by a male. Specific examples of these two effects will be provided in our discussion of terrestrial arthropod prezygotic paternal investment.

FIXED COSTS AND THE EVOLUTION OF PATERNAL CARE

How a male is able to apportion his resources to offspring may have important effects on the fitness conferred by paternal

VALUE OF
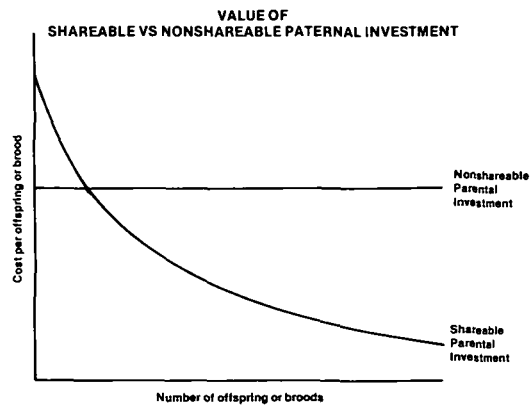SHAREABLE VS NONSHAREABLE PATERNAL INVESTMENT

FIG. 3. A graphic representation of the difference between shareable and nonshareable parental investment. Investment is shareable when the presence of additional offspring does not impinge on the benefits donated to each. Consequently, the expenditure per offspring declines monotonically with the number receiving benefits (modified from Wittenberger, 1979).

investment. Perrone (1975), Altmann et al. (1977) and Wittenberger (1979) distinguish two kinds of parental investment. Shareable investments are those made in individual offspring which do not reduce a parent's ability to invest concurrently in other offspring. By contrast, nonshareable investment varies in an ever increasing fashion with the number of offspring receiving benefits (Fig. 3). Because of the fixed nature of the costs involved, shareable paternal investment where it occurs may actually serve to increase the subsequent mating success of caring males. Females who pair with recently mated males risk reduced male parental investment if paternal investment is nonshareable. No such risk exists when paternal investments are shareable across broods. Nest defense provides a good example of shareable paternal investment since a male can probably guard several broods of offspring as effectively as one at no additional cost (Williams, 1975, p. 135). Moreover, from the point of view of female mating preferences, a well defended, occupied nest may prove most attractive (Ridley and Rechten, 1981). Females could profit from mating with males already defending a brood in two ways. First, the offspring of such males

are more likely to be the preferred mates of females (the sexy son hypothesis of Weatherhead and Robertson, 1979). Second, the probability of nest abandonment by a male should decrease with the number of broods he defends since the cost of nest guarding is fixed (C. W. Petersen, personal communication). Maynard Smith (1982) has modified his earlier payoff matrix (1977) to include the possibility that a male can increase his probability of an additional mating by providing his offspring with care. Clearly, male parental care is likely to be an evolutionarily stable strategy in such a situation.

General Comments on Paternal Care by Terrestrial Arthropods

Perhaps the best way of understanding why a rare phenomenon occurs when it does lies in identifying those factors which preclude its more regular occurrence. Such an approach seems appropriate in this case, given that male parental care occurs only rarely among the nearly one million species of terrestrial arthropods. We suggest two reasons for this low incidence of paternal care. First, terrestrial arthropod parents of both sexes have limited ability to enhance offspring survival, i.e., $P_0 \cong P_1 \cong P_2$. Precisely how this limitation affects parental care decisions is illustrated by the model presented earlier (Table 1). Obviously, this reasoning would predict an infrequent occurrence of any form of parental care by terrestrial arthropods. However, in those restricted cases where parental care does occur, a second explanation is necessary to account for the bias that exists toward maternal care. Clearly, this bias results from the differing parental care trade-offs experienced by males and females. We conclude this section by discussing those features of terrestrial arthropods which make parental care a more expensive option for males.

Parents can potentially increase the survival rate of their offspring by providing protection against predators and harsh physical conditions (reviewed for insects by Tallamy, 1984). The typically small size of terrestrial arthropods limits their ability to

defend themselves, or their broods, against an assortment of larger bodied predators and therefore restricts the number of cases in which parental care confers net benefits. This notion is consistent with those examples in which parental care does serve as an effective means of deterring natural enemies. Parental care significantly reduces offspring losses to parasites—which are generally smaller than their host species— in a diverse set of terrestrial arthropods, including certain assassin bugs (Bequaert, 1912; Ralston, 1977), sphecid wasps (Peckham, 1977; Coville and Coville, 1980), and earwigs (Schaller, 1968; Lamb, 1976). Proficiency at defending the eggs and larvae against predators appears to require some specific preadaptations on the part of the parents (Tallamy, 1984). For example, Wood (1978), Melber et al. (1980), and Eberhard (1975) have experimentally demonstrated effective predator deterrence in membracid treehoppers, acanthosomatid shieldbugs, and pentatomid bugs, respectively. Species in these three families are relatively large, heavily armored, and capable of covering most or all of a brood of offspring with their bodies.

Natural selection favoring egg care provides the critical step necessary for the evolution of more advanced forms of parental care. However, in the case of insects, an egg extremely well adapted for harsh physical conditions seems to have obviated the need for parental care of eggs (Smith, 1980). Under desiccating environmental conditions, the irregular surface of a terrestrial insect egg minimizes water loss while permitting the passage of sufficient oxygen through the egg chorion (Hinton, 1970, 1981). Examination of the surface morphology of a representative sample of arachnid eggs would prove useful in evaluating this hypothesis. The relatively frequent occurrence of maternal care of eggs in arachnids may stem from the vulnerability of eggs having minimal insulation against a desiccating environment. We further predict that convergence on the insect egg morphology has occurred with solpugid and opilionid eggs since females in these arachnid orders typically oviposit and then abandon eggs.

Investment in offspring represents just one alternative among an array of possible life history tactics available to a male. As previously mentioned, the infrequent occurrence of male parental care by terrestrial arthropods suggests that the returns on such investments are typically low. Why is this the case? We offer an explanation based on insights provided by population geneticists, on some general properties of terrestrial arthropod populations, and on sperm transfer patterns.

The evolution of senescence presented a problem for population geneticists who sought to explain the maintenance of this seemingly maladaptive phenomenon by natural selection (Charlesworth, 1980). From a demographic perspective, senescence occurs when an individual reaches a certain age and his chances of survival and reproduction begin to decline. This apparent paradox was resolved by recognizing that the intensity of natural selection decreases with increasing age (Bidder, 1932; Haldane, 1941; Medawar, 1952; Comfort, 1956; Williams, 1957; Hamilton, 1966; Rose, 1983). Consequently, natural selection would favor genes conferring early life history benefits despite the deleterious effects those same genes might manifest later in life (Williams, 1957; Charlesworth, 1980; Rose, 1983). Selection for such genes would obviously be most intense in species susceptible to high levels of what Charlesworth (1980) has described as "unavoidable mortality." Similarly, selection should favor genes coding for increased early survival and fecundity in populations which are increasing rapidly or which exhibit a prolonged increase phase followed by a period of more rapid decline (Caswell, 1982; Fig. 4). These processes can be invoked to explain both the evolution of senescence and the low incidence of terrestrial arthropod paternal care. Essentially, genes favoring early survival and fecundity are selected for at the expense of genes tied to preadaptations for paternal care.

Population structure leading to a high level of inbreeding can also play an important role in limiting expected returns on paternal care by terrestrial arthropods. As
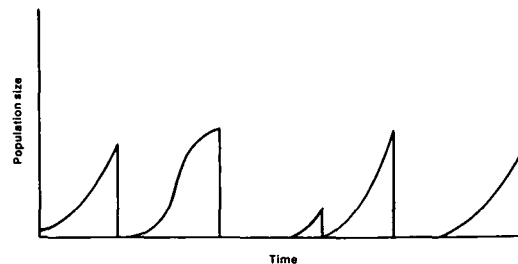

FIG. 4. One possible pattern of growth and decline in a nonequilibrium population. In this case, the populational crashes probably result from density independent mortality sources such as an abrupt seasonal change or some other physical catastrophe. Selection for genes conferring early life history benefits is particularly intense in populations exhibiting this type of dynamical behavior (after Caswell, 1982).

Hamilton (1967) has shown both theoretically and empirically, extreme inbreeding results in strikingly skewed sex ratios in favor of females. For example, in *Melittobia acasta* and *Acarophenax tribolii* females outnumber males by a factor of more than 20 (Hamilton, 1967). In such cases male competition for mates is nonexistent. Clearly, the prolonged development associated with attaining competitive size (Trivers, 1972; Warner, 1984) does not occur among males in highly inbred populations. On the contrary, selection favors rapid development of males to increase access to females (Wiklund and Fagerström, 1977). As a consequence of early maturation and the massive reproductive effort needed to inseminate many females, these males are precluded from investing in morphologies conducive to the prolonged survival necessary for the evolution of paternal care.

Finally, we suggest that sperm transfer patterns have equally important implications for the evolution of male parental care. Indirect spermatophore transfer without pair formation, which does occur in a variety of terrestrial arthropod species (Fig. 1; Schaller, 1971; Thomas and Zeh, 1984), dissociates a male from his offspring. The elimination of any possible link between parent and progeny which stems from this type of sperm transfer provides a definitive example of the association hypothesis previously discussed.

TABLE 2. *Parental investment by terrestrial arthropods.*[a]

Taxa	Category of investment				Comments
	Maternal	Prezygotic ♂[b]	Biparental care	Exclusive ♂ care	
Subphylum Chelicerata					
Class Arachnida					
Order: Scorpiones (scorpions)	OVO, VIV, YP Williams, 1969; Francke, 1979	MI Polis and Farley, 1979			♀ may eat males before mating occurs
Uropygi (whipscorpions)	BS, YC Weygoldt, 1972				produce brood sac
Schizomida (schizomids)	BS, YC Kaestner, 1968				produce brood sac
Amblypygi (tailless whipscorpions)	BS, YC Alexander, 1962; Weygoldt, 1970, 1972				produce brood sac
Araneae (spiders)	EP, EC, YC, YP, YR Kullman, 1972; Buskirk, 1981; Foelix, 1982	PI, MI Robinson, 1982; Foelix, 1982			all protect eggs with silk
Ricinulei (ricinuleids)	EC Kaestner, 1968				♀ carries egg under carapace
Pseudoscorpiones (false scorpions)	BS, YC, YP Weygoldt, 1969; Brach, 1978				produce brood sac
Solpugida (sun spiders)	EP Muma, 1966				bury eggs, otherwise no care
Opiliones (harvestmen)	EC, YC Mitchell, 1971; Forster and Forster, 1973			EC Rodriguez and Guerrero, 1976	typically oviposit and abandon
Notostigmata, Parasitiformes, Acariformes (Acari)	EP, EC, OVO, VIV Lipa and Chimielewski, 1966; Summers and Witt, 1972; Krantz, 1978				typically oviparous with no care

TABLE 2. *Continued.*[a]

Taxa	Maternal	Prezygotic ♂[b]	Biparental care	Exclusive ♂ care	Comments
Subphylum Crustacea					
Class Malacostraca					
Order: Isopoda					
Oniscoidea (wood lice)	VIV Heeley, 1941		YC, YP Linsemair and Linsemair, 1971, Schneider, 1975		brood eggs in marsupium
Subphylum Uniramia					
Class Chilopoda (centipedes)					
Order: Scutigerida	EP Lewis, 1981	GPI (ingest spermatophores) Lewis, 1981			eggs laid singly
Lithobiida	EP Lewis, 1981	GPI (ingest spermatophores) Lewis, 1981			eggs laid singly
Scolopendrida	EP, EC, YC Lewis, 1981				eggs laid in clutches
Geophilida	EP, EC, YC Lewis, 1981				eggs laid in clutches
Class Diplopoda (millipedes)					
Order: Polyxenida	EP Cloudsley-Thompson, 1968				oviparous, minor form of egg protection typically provided
Oniscomorpha	EP Cloudsley-Thompson, 1968				
Polyzonida	EP, EC Barnes, 1980				
Spirobolida	EP Kaestner, 1968; Shaw, 1966				
Iulidiformida	EP Kaestner, 1968			EC Kaestner, 1968	

TABLE 2. *Continued.*[a]

Taxa	Category of investment				Comments
	Maternal	Prezygotic ♂[b]	Biparental care	Exclusive ♂ care	
Chordeumatida	EP Barnes, 1980				
Polydesmida (flatbacks)	EP, EC Barnes, 1980				
Class Insecta (insects)					
Order: Plecoptera (stoneflies)	OVO Hynes, 1970				typically oviparous with no care
Embioptera (web spinners)	EC, YC Ledoux, 1958				♀ deposit eggs in silken chambers
Phasmida (stick insects)	EP Hetrick, 1949				a few bury eggs, most oviposit in open
Orthoptera (grasshoppers, crickets)	EC, YC, YP Wilson, 1971; Hinton, 1981	GPI, GPA, MI Gwynne, 1982, 1983, 1984a, 1984b; Field and Sandlant, 1983			maternal care atypical, PZ ♂ investment appears common
Dermaptera (earwigs)	EC, YC, YP Eickwort, 1981; Hinton, 1981		YC Chapman, 1917		maternal care of eggs relatively common
Isoptera (termites)			EC, YC, YP, YR Wilson, 1971		generally monogamous, all eusocial
Blattaria (cockroaches)	OVO, VIV, EC, YC Hinton, 1981	GPI, GPA Mullins and Kiel, 1980; Breed, 1983	EC, YC Cleveland *et al.*, 1934		maternal investment common; öotheca
Mantodea (mantids)		MI Roeder, 1935			eggs protected by öotheca
Pscoptera (book lice)	OVO, VIV, EP, EC				most oviparous
Mallophaga, Anoplura (lice)	OVO Eichler, 1946				typically oviparous with no care
Thysanoptera (thrips)	OVO, EC, YC Hinton, 1981; Mani and Rao, 1950				typically oviparous with no care

TABLE 2. *Continued.* [a]

Taxa	Category of investment				
	Maternal	Prezygotic ♂ [b]	Biparental care	Exclusive ♂ care	Comments
Homoptera (tree hoppers, planthoppers, aphids)	OVO, VIV, EC, YC Wilson, 1971; Wood, 1978; Hinton, 1981				egg and nymph defense relatively common in tree-hoppers
Heteroptera (true bugs)	EC, YC, YR (rare) Wilson, 1971; Melber and Schmidt, 1977; Eickwort, 1981	PI Carayon, 1964		EC, YC Smith, 1980	highest incidence of exclusive ♂ care by terrestrial arthropods
Coleoptera	EP, EC, YC, YP Wilson, 1971; Eickwort, 1981; Hinton, 1981	PI Matthes, 1962	EC, YC, YP, YR Wilson, 1971; Milne and Milne, 1976, Thornhill and Alcock, 1983; Halffter and Matthews, 1966		provisioning and biparental care highly developed in several species
Strepsiptera	larviparous Hinton, 1981				no care after larvae exit ♀
Hymenoptera (ants, bees, wasps)	EC, YC, YP, YR Wilson, 1971; Hinton, 1981				exhibit entire range of maternal investment strategies
Mecoptera (scorpionflies)		GPI, PI Thornhill and Alcock, 1983			PZ ♂ investment common
Diptera (flies)	VIV, EP, YR Hinton, 1981	GPI, GPA, PI, MI Thornhill and Alcock, 1983; Markow and Ankney, 1984			3 viviparous families, care atypical
Lepidoptera (butterflies, moths)	OVO Hinton, 1981	GPA Boggs and Gilbert, 1979; Boggs and Watt, 1981; Gwynne, 1984b			typically oviparous with no care
Class					
Onychophora (single order)	OVO, VIV Anderson, 1973	GPI (ingest spermatophores) Manton, 1938			most viviparous, a few oviparous

TABLE 2. *Continued.*[a]

| Taxa | Category of investment | | | | |
	Prezygotic ♂[b]	Maternal	Biparental care	Exclusive ♂ care	Comments
Class Pauropoda (single order)		EP, EC Harrison, 1914; Kaestner, 1968			most oviposit and abandon eggs
Class Symphyla (single order)		EP, EC Cloudsley-Thompson, 1968; Kaestner, 1968			oviparous

Abbreviations used: EP: "egg protection," performing a behavior to physically protect eggs (*e.g.*, wrapping in silk) and then abandoning them; EC: "egg care," remaining with eggs; BS: "brood sac," embryos nourished in external brood sac; OVO: ovoviviparous; VIV: viviparous; YC: "young care," remaining with larvae or nymphs; YP: "young provisionment," provisioning larvae or nymphs; YR: "young regurgitation feeding," includes trophyllaxis; GPI: "glandular product ingested," GPA: "glandular product absorbed," as indicated by radiolabelling study; PI: "prey item ingested"; MI: "male ingested."

[a] Recent reviews are cited in lieu of original papers where comprehensive information is available.

[b] We include only the transfer of nutritional substances by a male to his mate in this category.

SYNOPSIS OF PATERNAL INVESTMENT BY TERRESTRIAL ARTHROPODS

We conclude by providing an overview of three categories of paternal investment by terrestrial arthropods using specific examples to illustrate the selective factors leading to each type of investment. For a more comprehensive listing of parental investment by terrestrial arthropods, we refer the reader to Table 2.

Prezygotic paternal investment

A particularly pervasive feature of terrestrial arthropod reproductive behavior is the transfer of nutritional substances by a male to his mate (Thornhill, 1976; Thornhill and Alcock, 1983). Nutrients may be presented to the female in three ways: as a glandular product; as a captured prey item; or as a sacrifice of the male's own body. Glandular products take a variety of forms and may be consumed either directly by the female or absorbed through her reproductive tract. Females eat spermatophores in a variety of terrestrial arthropods, including centipedes (Klingel, 1960, 1962), onychophorans (Manton, 1938), and most commonly in orthopteran insects (reviewed by Gwynne, 1983). Other glandular products consumed by females include salivary (*Panorpa* scorpionflies, see Thornhill, 1981) and dorsal (cockroaches, reviewed by Breed, 1983) gland secretions. In Lepidoptera, glandular products are typically donated to the female through her reproductive system (Boggs and Gilbert, 1979). Male balloon flies (Kessel, 1955) on the other hand use prey lures on which the females feed during copulation. Hangingflies (Mecoptera, see Thornhill, 1977) and some spider species (*e.g.*, *Pisaura*, reviewed by Foelix, 1982) engage in comparable nuptial feeding habits. Finally, males in certain tropical mantid (Roeder, 1935), ensiferan orthopteran (Field and Sandlant, 1983), spider (Grasshoff, 1964; Blanke, 1975), and ceratopogonid midge (Downes, 1978), species do on occasion offer the most extreme form of nuptial gift by sacrificing their soma to their mates.

There is some debate, however, on

whether such prezygotic contributions to offspring through a male feeding his mate can be construed as a form of parental investment. Recently, several authors have addressed this question by attempting to partition a male's total reproductive effort (RE) into mating (ME) and parental (PE) components (Low, 1978; Alexander and Borgia, 1979). Alexander and Borgia (1979) assert that a male cannot expend effort on offspring prior to fertilization since the intent of such effort rests in the acquisition of a mate. By contrast, Trivers (1972) and Thornhill (1976) would interpret male prezygotic contributions as parental, given that such investments do influence the survivorship of offspring while incurring some cost to a male. Gwynne (1984b) approaches this problem by suggesting a third category of reproductive effort. He defines as nonpromiscuous, those mating efforts which include material or risk lowering benefits to a male's mate or offspring. Certain male prezygotic investments do, of course, function purely to attract a mate without conferring any benefits on offspring and must therefore be categorized strictly as mating efforts (ME). However, we would argue that from an evolutionary standpoint, the further distinction between paternal investment and nonpromiscuous mating effort is inappropriate. Regardless of whether an individual male operates in a certain way in order to attract a mate or because he wishes to benefit his offspring, natural selection acts only on results and can take no account of such differing intentions. We therefore conclude that prezygotic contributions to offspring by males can be interpreted as paternal investment. Consequently, the same approach adopted in the parental care model previously discussed is equally applicable to the evolution of pre- and postzygotic male investments in offspring. With either category of investment, selection favors contributions to offspring when the benefits—increased offspring survival (P) and enhanced paternal certainty (C)—outweigh the costs. Additionally, males investing prezygotically can derive benefits from increasing the fecundity of their mates.

A male who invests prezygotically can,

as previously mentioned, effect an increase in his paternal certainty by maximizing the number of sperm transferred. Thornhill (1980b) and Sakaluk (1984) have demonstrated the direct correlation that exists between the number of sperm transferred and the size of the nuptial gift. Moreover, experiments with doubly mated females demonstrate that the proportion of eggs fertilized by each male is a function of the amount of his investment (Sakaluk, unpublished data). Alternatively, a male can increase his paternal certainty by discouraging his mate from copulating with other males (Thornhill, 1976). In the hangingfly *Hylobittacus apicalis*, Thornhill (1980a) has shown that only a male who offers his mate a sufficiently large prey item can ensure that the female copulates with no other males before depositing eggs.

Because of the difficulties in demonstrating benefits to females and offspring from male prezygotic investment, few clear-cut examples have been recorded. Although failing to establish an incontrovertible link between female fitness and male prezygotic investment, a number of studies incorporating radiolabelling techniques have succeeded in demonstrating that male derived nutrients are incorporated into eggs (Boggs and Gilbert, 1979; Mullins and Kiel, 1980; Boggs and Watt, 1981; Schal and Bell, 1982; Markow and Ankney, 1984). To date, Gwynne (1984a) provides the only direct experimental evidence that nuptial feeding by a male increases the size and number of eggs produced by his mate.

Biparental care

Postzygotic investment in offspring by male terrestrial arthropods occurs most commonly in the context of biparental care and is marked by considerable variation in scope and complexity. At one extreme, male sphecid wasps provide no more than protection from parasites (Peckham, 1977; Coville and Coville, 1980; Hook and Matthews, 1980) as a byproduct of defending nest sites constructed and provisioned by females. Contributions by male burying beetles (*Nicrophorous*), by comparison, are extensive and complex. The mating pair together sequester a small animal carcass,

construct a brood chamber, and proceed to prepare the corpse for larval feeding (Pukowski, 1933; Wilson, 1971; Milne and Milne, 1976).

In situations in which uniparental care is essential to offspring survival, biparental care may well evolve if the opportunities for additional matings by males are poor, *i.e.*, if the costs of paternal investment are minimal. In the desert isopod *Hemilepistus reaumuri*, the male and female cooperate to build, clean and defend burrows (Linsemair and Linsemair, 1971; Linsemair, 1972; Shachak *et al.*, 1976; Shachak, 1980). The pair also engage in foraging expeditions outside the burrow and generally share responsibilities in the care of the young. Interestingly, this high level of paternal investment has apparently evolved in a context in which the male has essentially no chance of remating. At his most vulnerable during a search for a partner (63–97% mortality rate during pair formation, see Shachak, 1980), the male has only a brief mating season in which to find a receptive female. His opportunities for additional matings are further reduced because widowed pregnant females and those with young do not accept new partners (Linsemair and Linsemair, 1971). The similar circumstances encountered by termite males may explain their convergent parental investment patterns. These observations are consistent with the theoretical prediction that selection can favor synchronous female reproduction as a means of increasing male parental investment (Knowlton, 1979). Indeed, females should generally employ all means at their disposal to promote male involvement in parental care.

Restrictions on promiscuous matings by males may be an important first step in the evolution of biparental care. Given such mating constraints, natural selection should favor male adaptations to enhance offspring survival. As a consequence, when ultimately P_2 greatly exceeds P_1 an evolutionarily stable parental care strategy will have been established. Enhanced offspring survival can generally be achieved by the increased level of nonshareable investment made possible by biparental care. Typi-

cally, such investments are those directed toward larvae or nymphs, as opposed to eggs. The expropriation of a food resource for provisioning the young is a common form of nonshareable parental investment exhibited by terrestrial arthropods. Given that numbers of offspring are limited by the quantity of food provided, the involvement of both parents in provisioning can significantly increase surviving offspring. In contrast to the above situation in which both parents engage in the same parental care activities, the most complex forms of biparental care are characterized by a division of labor in which males and females take differing responsibilities. The desert isopod *H. reaumuri*, in which one parent defends the nest while the other forages, provides a particularly good example of this complementary type of biparental care. Cooperation between male and female is particularly significant when competition for larval food is intense. It is probable that this competitive pressure has been a major force in the evolution of biparental care in dung and burying beetles (Milne and Milne, 1976; Heinrich and Bartholomew, 1979; Tallamy, 1984), both of which sequester food. By taking advantage of environmental circumstances and refusing copulation until the corpse or dung has been secured, females of these species succeed in exacting considerable assistance from males.

Exclusive paternal care

While it is common for females to assume sole responsibility for postzygotic contributions to offspring among those terrestrial arthropod species engaging in parental care, males do so only rarely. Most of the 100 or so species displaying male uniparental care belong to the family of giant water bugs Belostomatidae, a group recently derived from terrestrial arthropods, while the remaining examples of this type of care are scattered among diverse arthropod lineages. In marked contrast to the often varied and complex services provided to offspring when both parents participate, exclusive paternal care is limited in scope. In the context of uniparental care, males usually restrict their activities to pro-

tecting eggs, although occasionally for brief periods, clusters of newly emerged nymphs are protected from enemies or the rigors of the physical environment. Males are known to actively defend batches of eggs against natural enemies, typically parasites, in the tropical assassin bugs *Rhinocoris albopilosus* (Odhiambo, 1959, 1960), *R. albopunctatus* (Nyiira, 1970), and a *Zelus* sp. (Ralston, 1977) and in the opilionid harvestman *Zygopachylus albomarginis* (Rodriguez and Guerrero, 1976). An elaborate form of exclusive paternal care has evolved in some belostomatid water bugs. Females oviposit on the backs of the males who then safeguard the eggs from fungal infections, desiccation, metabolite poisoning and low dissolved oxygen concentrations (Smith, 1976*a*, *b*).

Examples of exclusive paternal care by terrestrial arthropods appear to have developed along an evolutionary pathway consistent with the association hypothesis. Assassin bugs (Odhiambo, 1959, 1960; Nyiira, 1970; Ralston, 1977), harvestmen (Rodriguez and Guerrero, 1976) and millipedes (cited in Kaestner, 1968) engage in exclusive male care which probably has evolved out of simple mating site attachment (territoriality) by males. Based on the incomplete data available, we would predict that male single parent care, originating by the same means, occurs in the flat bug *Neuroctenus pseudonymus* (McClure, 1932) and in the secondarily aquatic water striders, *Rhagadotarsus* and *Halobates* (reviewed by Smith, 1980). Mating site attachment by the male, and prompt oviposition by the female on this mating site combine to lower the cost of paternal care so that it becomes an evolutionarily stable strategy. Indeed, as argued earlier, if a male provides some shareable form of parental care, as for example in egg defense, such care could even act to increase his subsequent mating success. Nest guarding serves the coinciding interests of both male and eggs by simultaneously providing protection and enhancing a male's attractiveness. An example of this effect may occur in harvestment in which some of the nests defended by males receive no eggs while others nearby are visited repeatedly by ovi-

positing females (Rodriguez and Guerrero, 1976).

An alternative evolutionary route to exclusive paternal care, once again consistent with the association hypothesis, has been followed by belostomatids (Smith, 1980). In this case, male parental care seems to have grown out of repeated copulation and protracted mate guarding. Since consideration of the evolutionary steps involved in the development of paternal care in these water bugs lies, strictly speaking, beyond the boundary of this treatment of terrestrial arthropods, the reader is referred to Smith (1980) for a more detailed discussion. As a final note, we suggest that the pathway to exclusive paternal care via mate guarding has been responsible for the evolution of the poorly known egg carrying behavior of the male coreid bug, *Phyllomorpha laciniata* (Jeannel, 1909).

CONCLUSIONS

Why do males of terrestrial arthropod species generally desert rather than invest in their offspring? When males do contribute to offspring, what determines the context—prezygotic, biparental, or exclusive paternal—of male involvement? These are the two major questions underlying our synopsis of paternal investment by terrestrial arthropods. It seems evident that an interplay between small size, high mortality rates, and extreme sensitivity to the physical environment weighs heavily against the evolution of terrestrial arthropod paternal care. In general, fitness for the small, short-lived, vulnerable male lies in maximizing the number of females he fertilizes. He achieves this through early maturation and desertion. Only when unrestricted promiscuous mating is denied him, or when parental contributions can be used to attract new females, is the male terrestrial arthropod likely to be drawn into investing paternally.

In the absence of comprehensive experimental data our aim in this paper has been to present general hypotheses to account for paternal investment patterns in terrestrial arthropods. Verification or rejection of these hypotheses must await more

detailed experimental investigations into this, as yet, little explored area of terrestrial arthropod evolution.

Acknowledgments

We wish to thank D. N. Byrne, J. A. Buttle, V. Delesalle, W. L. Nutting, C. W. Petersen, R. H. Thomas, F. G. Werner, and M. Zeh for providing critical comments on initial drafts. We are especially grateful to Chris Petersen for his influential manuscript on paternal certainty and for other valuable insight and inspiration. This paper also benefited from our conversations with Scott Sakaluk and Steve Shuster. Finally, we owe the greatest debt to Jeanne Buttle who succeeded in convincing us that complex ideas can (and should) be explained in a straightforward manner.

D. Zeh gratefully acknowledges the receipt of a Sigma Xi Graduate Travel scholarship to attend this symposium.

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