



Stepparental Behavior as Mating Effort in Birds and Other Animals

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In many animal species, widowed or divorced parents may remate before young of the prior union are independent. In such circumstances, stepparents may kill their predecessors' offspring, may tolerate them without providing care, or may invest in them more or less as genetic parents do. Rohwer proposed that all three of these responses may be understood as mating tactics, adapted to different social and ecological circumstances. We discuss the selection pressures that would favor each of these alternatives and review relevant evidence on nonhuman stepparenting, especially in birds. Stepparental tolerance and (partial or full) care, which are the predominant human responses, are common in nonhuman animals too, and in many cases there is evidence supporting their interpretation as stepparental mating effort adaptations. In general, however, this interpretation is not as well established for tolerance and care as it is for stepparental infanticide. Because tolerance and care are not distinct modes of behavior peculiar to stepparents, the hypothesis that they are nonadaptive by-products of parental psychology often remains tenable. We discuss the kinds of evidence needed to choose between by-product and stepparental adaptation hypotheses. © 1999 Elsevier Science Inc.

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Folklore portrays human stepparents as cruel and lustful (Thompson 1955), and they indeed abuse children both physically and sexually at vastly higher rates than genetic parents (Daly and Wilson 1988, 1996, 1998). Nevertheless, most stepparents neither abuse nor molest their stepchild-

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dren. Instead, they tolerate and even care for them, often investing much time and resources in promoting the children's well-being. The Darwinian rationale for expecting stepparents to be uncaring and exploitative relative to genetic parents is obvious: the survival and eventual reproduction of one's stepchildren contribute nothing to one's direct fitness. A more puzzling question is why stepparents are so willing to undertake prolonged and apparently costly investments in their predecessors' young.

The hypothesis that such alloparenting represents "misdirected" care in a social context differing from that in which our parenting adaptations evolved is plausible for modern adoption by nonrelatives, but not for stepparenting. In foraging societies without modern medicine and technology, premature death and divorce are common, as is remarriage (Hewlett 1991). The problem of how to allocate one's efforts in such a situation must have confronted hundreds of the ancestors of every person now living.

In nonhuman animals, stepparental benevolence often is best interpreted as "mating effort," with the payoff coming not from enhanced fitness of the benefited young, but from enhanced prospects of future reproduction with their genetic parent (Rohwer 1986). Recent analyses support the idea that stepparental investment functions as mating effort in the human animal as well (Daly and Wilson 1998; Lancaster and Kaplan 1999).

In a sense, the "mating effort" interpretation has solved the puzzle of stepparental "altruism." Indeed, this idea is now so well entrenched that even the "paternal" behavior of genetic fathers is sometimes interpreted as mating effort (Freeman-Gallant 1998; van Schaik and Paul 1996). But why is stepparental behavior so variable across animal species, such that stepoffspring are routinely killed in some species, are tolerated but ignored in others, and are the recipients of extensive alloparental investment in still others? Rohwer (1986) proposed that variations in ecology, demography, and life history could explain this diversity, and our main concern in this article is to consider the current status of his argument and to extend it, in light of what is now known about the behavior of nonhuman stepparents.

From the early 1970s, when infanticide in primates was convincingly interpreted as a form of male-male sexual competition (Hrdy 1974), through the middle 1980s, behavioral ecologists paid little attention either to documenting stepparental tolerance and care of dependent offspring or to developing an interpretation of these behaviors. Yet, noninfanticidal responses to unrelated dependent offspring are common in a wide variety of species, particularly among birds.

Most of the research on nonhuman stepparenting has been conducted with birds. More than 90% of the world's avian species are socially monogamous, and both mates typically care for the young. Levels of adult mortality while nesting may be sufficiently high that remating during the period of offspring dependency has been selectively significant. In the first review of birds' responses to the dependent offspring of newly acquired mates, Rohwer (1986) found that tolerance and care had been reported more often than infanticide. Just four experimental studies of avian stepparental behavior had then been conducted, and none reported infanticide (Martin in Rohwer 1986 [now Martin 1989]; Power 1975; Rohwer 1985; Weatherhead and Robertson 1980). Moreover, the weight of a large body of nonexperimental evi-

dence also fell toward tolerance and care, rather than infanticide. Rohwer's achievement was to show that various combinations of life history traits (including sex ratio imbalances, double broodedness, renesting dispersal, and season-to-season pair bonds) can make tolerance and care of a new mate's preexisting dependent offspring the best available mating strategy.

Many other taxa, including fish, mammals, and insects, also include species with biparental care and thus are appropriate for studies of stepparenting. Carion beetle pairs, for example, defend a buried carcass and feed predigested bits to their larvae; usurpers of either sex may kill their predecessors' young and replace them with their own (Robertson 1993). About 5% of the 422 bony fish families include species with biparental care (Gross and Sargent 1985), and the responses of stepparents vary. In monogamous anemonefish, which live in close symbiotic association with sea anemones, removal experiments and field observations indicate that stepfathers are not infanticidal; instead, they tolerate or care for their new mate's preexisting eggs (Yanagisawa and Ochi 1986). Many cichlid species are biparental, but experimentally widowed parents typically will not pair again unless and until brood care is complete (Keenleyside 1991), presumably because replacement mates would be infanticidal. In some species, widowed males abandon their broods if unmated females are abundant, indicating sensitivity to alternative breeding opportunities and/or to the threat of infanticide; there is no evidence that females respond to the shortage of males in this situation by becoming willing stepmothers (Keenleyside 1983; Balshine-Earn 1995).

Here we update the review by Rohwer (1986). We also try to generalize the theoretical discussion beyond the specifics of bird biology, so that it will apply to any species with biparental care, but it is still only the bird literature that we have attempted to review thoroughly. Our goals are to identify key issues that must be addressed if tolerance and care of unrelated offspring are to be interpreted as adaptive mating effort and to illustrate how these issues can be addressed by discussing examples of recent experimental work.

TERMINOLOGY

Rohwer (1986) referred to the stepparent's caregiving option as "adoption." This choice of words was unfortunate, because adults adopt unrelated young in contexts other than stepparenting, and the word's principal connotation is "adoption by strangers," that is, by a pair of nonrelatives. Sargent (1989) compounded the confusion by calling male minnows that steal eggs and use them to attract new females to spawn in their nests "stepfathers," even though this mating effort was not directed at the stolen eggs' mothers.

Here, we shall adhere to terms more in keeping with ordinary English meanings: a stepparent is an individual who has acquired a mate with preexisting dependent offspring, whereas an adoptive parent is one who provides parental care to young that are neither its own genetic offspring nor its mate's (Table 1). This terminology has several advantages. First, it renders transparent the presumed genetic re-

Table 1. Suggested Terms for Alloparental Behaviors Related to Mating Effort

Term	Definition
Stepparent	An individual who has acquired a mate with preexisting dependent offspring.
Adoptive parent	An individual who provides parental care to young that are neither its own genetic offspring nor its mate's.
Courtship kidnapper	An individual who attempts to attract a mate by acquiring unrelated dependent offspring and caring for them.
Caregiving usurper	An individual who attempts to disrupt a pair and usurp a mate with preexisting dependent offspring by caring for them.
Infanticidal usurper	An individual who attempts to disrupt a pair and usurp a mate with preexisting dependent offspring by killing them.

relationships among the parties in question. Second, “stepparent” automatically identifies the social relationship of the focal animal to both its new mate and the new mate’s dependent offspring. Finally, the adoption of young unrelated to either parent is distinguished from stepparenthood. (Ambiguity in this regard is a source of confusion in estimates of the incidence of human adoption, because a large proportion of adoption decrees are granted to a stepparent plus genetic parent.)

Table 1 also offers suggested terms for three related forms of mating effort. First, a “courtship kidnapper” is an individual who tries to attract mates by stealing unrelated dependent offspring and caring for them, as has been documented in fish with male care of young (Rohwer 1978; Wootton 1971). A courtship kidnapper may steal eggs for transfer to his own nest (Mori 1995), evict a parental male and take over an entire nest (Unger and Sargent 1988), or simply adopt orphaned young (Jewell 1968; Unger and Sargent 1988). He then uses these young or his caretaking as a courtship display. Second, a “caregiving usurper” is an individual who attempts to disrupt a pair and usurp a mate with preexisting dependent offspring by caring for the young. By providing care superior to that offered by the genetic parent, the caregiving usurper attempts to convince his prospective mate that she should oust her present mate. Such usurpation may be most common in helping and cooperatively breeding bird species in which individuals queue for mating opportunities (Clarke 1989; Cockburn 1998; Reyer 1990; Zahavi 1995). Third, an “infanticidal usurper” is an individual who attempts to disrupt a pair and usurp a mate with preexisting offspring by killing the dependent young. This strategy, documented in birds (Chek and Robertson 1991; Crook and Shields 1985; Hotta 1994; Møller 1988a; other anecdotes summarized in Rohwer 1986), succeeds when reproductive failure induces divorce, making a mate or nest site available to the perpetrator. Because courtship kidnapping, usurpation by caregiving, and usurpation by infanticide are not stepparenting, we will not discuss them further.

DO ANIMALS POSSESS BEHAVIORAL/PSYCHOLOGICAL ADAPTATIONS FOR STEPPARENTHOOD?

A stepparent has a range of options for how to treat the preexisting dependent offspring of its newly acquired mate: kill them, tolerate them without actively invest-

ing, or care for them. Once we have identified the option(s) chosen by stepparents in a particular species, our challenge is to assess whether their behavior reflects stepparenthood-specific adaptations. Was the behavior selected for in previous generations in the specific context of stepparenting because it increased the fitness of stepparents, or is it a by-product of selection in other contexts, such as genetic parenthood? One relevant consideration in addressing these questions is how often individuals became stepparents in previous generations. Another is how closely stepparents' behavior resembles that of genetic parents, and whether the distinctions present the appearance of special purpose "design."

Infanticide typically is so distinct from the behavior of genetic parents that one immediately suspects it is an adaptation to the specific circumstance of stepparenthood. The idea that such infanticide represents a sexually selected adaptation continues to elicit hostile criticism (Bartlett et al. 1993; Dagg 1998), but these critiques invariably entail misunderstandings, e.g., that an infanticidal adaptation must exhibit appreciable heritability or must be beneficial not just on average but in every case. Once it has been shown that stepparents routinely and efficiently commit infanticide, that by so doing they hasten their own reproduction, on average, and that they incur no detectable costs, the case has been made (Pusey and Packer 1994; Sommer 1994).

For species in which significant parental investment is the norm, tolerance of unrelated young by stepparents may be distinct enough from the behavior of genetic parents to suggest that it too is an adaptation specific to stepparenting. However, because the amount of care provided and the relative contributions of mothers versus fathers may vary considerably across pairs of genetic parents within a species, whether stepparental tolerance is a discrete mode of behavior often is ambiguous.

Most difficult to interpret is stepparental caregiving. Without further analysis, the most parsimonious explanation is that such behavior represents a misdirection of normal parental care (Rohwer 1986). More specifically, caregiving by stepparents has three possible interpretations. It may be nonadaptive simply because selection has not fashioned a discriminative stepparental response; it may be a nonadaptive result of deception or confusion about parenthood (Gjershaug et al. 1989); or it may constitute adaptive mating effort, which pays off in future matings with the stepoffspring's genetic parent (Rohwer 1986) and/or with other future mates (Gori et al. 1996; Rohwer 1985).

Any evidence that the behavior of stepparents is contingent on cues that are statistically associated with parenthood is evidence that individuals have evolved the ability to distinguish, at least operationally, between their own and other offspring. When such evidence exists, then tolerance and caregiving warrant further investigation, because they cannot readily be dismissed as errors of parental investment. But even when there is no obvious difference between the behavior of stepparents and genetic parents, we cannot assume that selection on stepparental inclinations has been ineffective or absent. In this circumstance, a comparative approach may offer the only means of evaluating whether adaptation to the demands of stepparenting exists (Rohwer 1986).

Details of the natural history of a species sometimes can be exploited to distinguish stepparental adaptation from error experimentally. In the polygynous yellow-

headed blackbird, for example, fathers normally feed only the oldest chicks on their territory, presumably because they have the highest reproductive value (Willson 1966). Thus, Gori et al. (1996) could remove fathers after their primary mates had completed their clutches, to see how replacement males would treat older young they had not sired versus younger nestlings that they should have sired. The stepfathers did not naively follow the rule “feed the oldest chicks,” even though they had clearly discovered the nests containing those chicks. Instead, stepfathers fed the eldest brood they had sired (Gori et al. 1996), demonstrating an ability to distinguish between their own and other offspring.

KEY QUESTIONS ABOUT STEPPARENTS

The prospective analysis of the behavior of stepparents made by Rohwer (1986) can be generalized away from the specifics of avian biology by addressing nine questions. We list these key questions in Table 2 and suggest the implications of different answers with respect to selection on stepparental behavior.

The most difficult question to address for most animals is often the first: Can the stepparent discriminate, even probabilistically, between its own and other offspring? When a stepparent kills its new mate’s preexisting offspring, then cares normally for its own offspring, it answers this question for us. As a result, infanticidal behavior often more readily is interpreted in terms of selection and adaptation than is stepparental tolerance or caregiving. Indeed, studies of infanticide require so little comment that Table 3 merely lists the experimental studies of birds of which we are aware, without further discussion. It is when stepparents let the young live that clever experiments may be necessary to determine whether their behavior reflects adaptation specific to the stepparental situation.

The recent revolution in paternity exclusion techniques and studies has made it clear that male parental care often is contingent on cues indicative of the probability of paternity (Table 2, Question 2). Males in many species seem to follow an all-or-nothing rule, showing full parental care if available cues indicate some (threshold?) possibility that they have fathered the young in question, but otherwise giving no care at all. Stepparents not offering care may kill (Table 3) or tolerate (Table 4) their stepoffspring. In only a few bird species, such as barn swallows (Møller 1988b), dunnocks (Davies et al. 1992), reed buntings (Dixon et al. 1994), white-browed scrub wrens (Whittingham and Dunn 1998), and Smith’s longspurs (Briskie et al. 1998), are males known to make finer adjustments to match the level of care they provide to their probability or probable share of the brood’s paternity (Kempnaers and Sheldon 1997; Whittingham et al. 1992).

Key questions facing both male and female stepparents are whether new mates are sufficiently scarce that care or tolerance might be an acceptable cost of courtship (Table 2, Question 3); whether a newly established pair may be expected to endure, and for how long (Question 4); and whether an individual that loses its existing offspring will quickly return to breeding condition (Question 5). Almost all birds will lay replacement clutches, so the first glance answer to Question 5 for most bird spe-

Table 2. Key Questions for Interpreting Stepparental Behavior and the Implications of a “Yes” or “No” Answer

Questions	“Yes” favors. . .	“No” favors. . .	Interpretations
1. Can stepparent operationally distinguish own from other young (by phenotype, timing, or other cues)?	Infanticide (or tolerance)	Caregiving	If stepparent cannot discriminate, caregiving may represent misdirected parental care.
2. Is there any chance that the “stepparent” is actually genetic parent?	Tolerance (if slight chance) Caregiving (if greater chance)	Infanticide	If probability of parenthood >0, caregiving may represent parental investment.
3. Are replacement mates scarce?	Caregiving (or tolerance)	Infanticide	If yes, new mate has leverage to “demand” investment.
4. Are matings often of substantial duration?	Caregiving (or tolerance)	Infanticide	If yes, present mating effort can pay off later.
5. Can the new mate breed again quickly?	Infanticide	Tolerance (or caregiving)	If no, tolerance may entail little cost.
6. Does reproductive failure raise the chance that new mate will desert/divorce?	Caregiving or tolerance	Infanticide	Caregiving may be mating effort directed at new mate, especially if answer to Q3 is also yes.
7. Does caregiving reduce the new mate’s likelihood of seeking extra-pair copulations in future?	Caregiving	Tolerance or infanticide	Caregiving may be mating effort directed at new mate.
8. Will new mate’s reproductive failure discourage other potential mates?	Caregiving or tolerance	Infanticide	Caregiving may be mating effort directed at other potential mates.
9. Will the new mate’s future reproductive value be reduced by the investment required to fledge present young?	Infanticide or caregiving	Tolerance	Caregiving may be mating effort that maintains new mate’s reproductive value enough to compensate for cost.

cies is “yes.” However, we caution that rapid clutch replacement generally is documented only for well-established pairs, and newly formed pairs may not produce replacement clutches as quickly. Establishing whether they can and will do so generally requires experiments.

If a new mate can breed again quickly, the next question facing stepparents of both sexes is whether reproductive failure will cause the new mate to desert (“divorce”) the stepparent (Question 6). If not, or if another mate can readily be attracted to the stepparent’s new territory, then infanticide is to be expected, but if reproductive failure provokes divorce and thus precludes future breeding with the new mate, then tolerance or care may be a more effective form of mating effort. Stepparental caregiving also could function as mating effort by decreasing the probability that the genetic parent will cuckold the stepparent during future breeding attempts (Freeman-Gallant 1998; Question 7).

In polygynous species, stepparents face a further complication. Will destruction of the new mate’s brood discourage other potential mates from joining the

Table 3. Experimental Studies of Stepparental Infanticide

Species	Key questions addressed?	References
Wattled Jacana (females infanticidal)	No evaluation of likelihood of divorce	Emlen et al. 1989
Little swifts (females and males infanticidal—these cases are different from the mate thefts discussed in text)	If divorce occurs, reproductive failure does not discourage other potential mates (nests are time consuming to build and there are many floaters of both sexes)	Hotta 1994
Acorn woodpecker (females and males infanticidal)	Paternal discrimination and paternity assessment possible (removed dominant males destroy clutches; removed subordinates do not); Maternal discrimination possible (removed females destroyed clutches); Divorce impossible (no empty territories)	Koenig 1990
Tree swallows (females and males infanticidal)	Divorce unlikely (nest sites limited)	Robertson and Stutchbury 1988; Robertson 1990; Chek and Robertson 1991
Barn swallows (males infanticidal)	Divorce unlikely (nests time consuming to build)	Møller 1988A; see also Crook and Shields 1985
Tropical house wrens (females and males infanticidal)	Divorce appears unlikely (territories occupied continuously)	Freed 1986, 1987A, 1987B
North-temperate house wrens (males infanticidal)	If divorce occurs, reproductive failure does not discourage other potential mates (female-worthy territories may be limited)	Kermott et al. 1991
European starling (males infanticidal)	Divorce unlikely (nest sites limited)	Smith et al. 1996
House sparrows (males infanticidal)	Divorce unlikely (nest sites limited)	Veiga 1990, 1993

In every case, researchers established that the biological parent will breed again quickly with the infanticidal stepparent.

harem? When this is the case, care or tolerance may function as mating effort directed at other potential mates (Table 2, Question 8). For yellow-headed blackbirds, Gori et al. (1996) showed that territories with failed nests attracted far fewer new mates than territories where there were no failed nests. This study was not experimental, so confounding factors involving mate and territory quality cannot completely be dismissed, but the use of pairs of territories, matched for prior harem sizes, probably eliminated most potential confounds.

Finally, for stepparents whose new mate will not breed again quickly but may remain in the new pair-bond across years, we must ask if the new mate's residual reproductive value is being diminished by the costs of present care (Table 2, Question 9). If so, then stepparental care could be adaptive because it reduces the burden and helps maintain a new mate's reproductive value. No such case has yet been argued,

Table 4. Experimental Studies Documenting Stepparental Tolerance or Care

Species	Sample Size	Reference
Anemone fish	22 stepfathers were exposed to eggs or young; most showed full parental care	Yanagisawa and Ochi 1986
American kestrel	8 stepfathers and 1 stepmother tolerated eggs, but all broods failed	Bowman and Bird 1987
Willow ptarmigan	No infanticide by 49 replacing males; 14 of these that lacked primary broods behaved like fathers	Martin 1989
Black-billed magpie	28 males removed; all 9 stepfathers cared for young	Dunn and Hannon 1989
Mountain bluebird	8 stepfathers tolerated young; one stepmother cared for them	Power 1975
Western bluebird	9 stepfathers tolerated young (two of these fed young rarely)	Dickinson and Weathers 1999
Eastern bluebird	17 stepfathers tolerated young; 5 of these fed young occasionally	Meek and Robertson 1991
White-throated sparrow	10 stepfathers tolerated nestlings, at least briefly	Whillans and Falls 1990
Seaside sparrow	About 33 stepfathers tolerated eggs or young; all had primary broods and none provided care to stepbrood	Greenlaw and Post 1985
Savannah sparrow	22 stepfathers tolerated young; just a few (and only those without a primary brood) apparently provided some care	Weatherhead and Robertson 1980; Freeman-Gallant 1998
Yellow-headed blackbird	39 stepfathers tolerated eggs or young	Rutberg and Rohwer 1980; Gori et al. 1996
Red-winged blackbird	15 stepfathers tolerated young	Rohwer 1985

but the well-documented tradeoffs between current and future reproduction (Gustafsson and Pärt 1990; Nilsson and Svensson 1996; Røskaft 1985) make it a logical possibility. Of course, infanticide also could maintain a new mate's reproductive value by terminating costly parental investment, so this consideration appears to be unique in selecting against noninvesting tolerance and in favor of the extremes: either kill the young or help raise them.

REMOVAL EXPERIMENTS IN WHICH STEPPARENTS EXHIBITED TOLERANCE AND CARE

We are aware of experimental studies of 12 biparental species in which the majority of stepparents exhibited tolerance or care (Table 4). In this section we briefly review these studies and consider the degree to which they succeeded in addressing the questions listed in Table 2. In addition to these studies, observers have reported stepparental care and tolerance after naturally occurring replacements in many species of birds. We have not attempted to review all such nonexperimental reports, but some are referenced here and others by Rohwer (1986) and by Meek and Robertson (1991).

Anemomefish (*Amphiprion clarkii*)

Parental care in anemomefish includes guarding, fanning, and cleaning eggs. Males typically provide more care than females, especially as hatching approaches. In the removal experiment of Yanagisawa and Ochi (1986), one of 22 replacement males committed infanticide by eating his new mate's eggs while she was away from the nest. Females typically produce several clutches per season, so it is possible that infanticide could induce rapid renesting (Question 5). On the other hand, females may require substantial time to yolk new eggs, and the replacing fish may not be sexually mature.

Most of the other replacement males provided care indistinguishable from that of genetic fathers, but some took several days to reach this level. Three males provided partial care, but never exceeded the amount of care provided by the female, and two males that became stepfathers so late in the breeding season that relaying by their new mates could not be expected provided no care. In other cases, females widowed late in the season failed to attract replacements at all.

Steppaternal effort evidently varies in relation to the probability that the new mate will breed again, suggesting that an adaptive strategy is at work. However, a stepfather's options may be limited. Anemomefish mature as males and change sex only after further growth, so there is an excess of males (Question 3) and they are much smaller than females. Yanagisawa and Ochi (1986) suggest that mothers can bully stepfathers into providing care, but the fact that males who became stepfathers late in the season withheld care suggests that males retain some choice in the matter. Whether females are likely to divorce males that withhold care or are caught eating the eggs is unclear (Question 7).

American kestrel (*Falco sparverius*)

Stepparents in raptors are prone to caregiving and/or tolerance. If these behaviors reflect a stepparental adaptation, it is probably because of benefits that accrue over the duration of multi-year pair bonds (Question 4). That is, caregiving by a stepparent probably prevents its newly acquired mate from divorcing (Question 7). However, no study satisfactorily addresses this issue; most reports are anecdotal (references in Grubb et al. 1988; Rohwer 1986; Simmons 1992).

The only experimental study on raptors involved removal of both male and female American kestrels during incubation (Bowman and Bird 1987). One of four widowed males attracted a replacement, and all four (including the new pair) quickly abandoned the eggs laid by the male's previous mate. Eight of 16 widowed females attracted new males that courted, fed, and copulated with their new females just as prospective genetic fathers do, but, unlike genetic fathers, none of the stepfathers incubated the eggs, and all nests failed.

After the original clutches died, Bowman and Bird (1987) removed them from the nest boxes and four females renested with their replacement males. Most raptors will lay replacement clutches (Morrison and Walton 1980), so stepparental tolerance and care are puzzling and remain to be interpreted. Rohwer (1986) suggested that

newly formed pairs may be unable to produce fertile eggs in the current year (Question 5), but in the study by Bowman and Bird (1987), the four newly formed pairs that renested laid and hatched fertile eggs; however, none of the four succeeded in fledging young, suggesting that newly formed pairs may be limited in their reproductive abilities, perhaps because coordinated biparental care requires familiarity. Rohwer (1986) also proposed that the value of forming pair bonds and gaining a breeding site for future years (Questions 3 and 4) is critical to the lack of infanticide in raptors, a possibility that has yet to be tested.

Willow ptarmigan (*Lagopus lagopus*)

The study by Martin (1989) is thoroughly puzzling and may well represent an instance of misdirected parental care. Willow ptarmigans are mildly polygynous and territorial. Monogamous males help attend to the precocious brood, whereas polygynists typically assist only their primary mates. Martin observed the behavior of 49 replacement males, none of which committed infanticide. About one third of these males became replacements by expanding their territories and becoming polygynists. These males were fathers to the young of their primary mates and stepfathers to the young of their secondary mates, and they provided care only to their probable genetic offspring. The rest of the replacements were from the floating population. These males were apparently stepfathers only (paternity was not evaluated), but they provided full parental care. It is this behavior that is puzzling.

Female willow ptarmigan lay replacement clutches after egg-stage failures (Question 5), and they show no tendency to move to new territories within seasons in response to nest failures (Question 7). Females also remove cracked eggs from their nests, so stepfathers, which are considerably larger than females, should have been able to commit infanticide. For all of these reasons, infanticide should be expected (Martin 1989). Martin also sought evidence that benefits accrue to caregiving stepfathers in subsequent years and found none: they were no more successful in acquiring either territories or mates (Question 7), and in only one of 11 cases did a helped female breed the following year with the helpful stepfather (Question 4, rendering Question 9 moot). Twenty percent of the caregiving stepfathers became biological fathers of replacement broods after their mate's first brood was preyed on. These stepfathers were the only ones receiving any identifiable benefit. Apart from paternity not being evaluated, this study is exemplary for recognizing and addressing the puzzling care shown by stepfathers.

Black-billed magpie (*Pica pica*)

Dunn and Hannon (1989) removed 28 male magpies in an effort to compare the nesting success of single mothers versus pairs. Nine stepfathers, eight of which could not be caught for removal, showed full care, as had been seen in nonexperimental studies of magpies (Buitron 1988; Shannon 1958). At least four stepfathers replaced their predecessors after the female was no longer fertile, so their caretaking

cannot be attributed to partial paternity of the brood (unless they were cuckolders). Established pairs renest after failures, but never raise two broods in the same year (Question 5), which should favor stepparental infanticide. Between-season effects, however, may favor stepparental care to establish and maintain either long-term pair bonds or territory ownership (Question 4). In Europe, Baeyens (1981) found that pairs on high-quality territories tended to remain there year after year, without divorce, but pairs on poor territories often broke up if the male had the opportunity to join a widow on a high-quality territory. American birds seem to do the same (Dhindsa and Boag 1992).

Mountain bluebirds (*Sialia curruoides*)

Power (1975) observed neither infanticide nor parental care on the part of eight male mountain bluebird stepfathers (of 12 experimental removals), but observations were limited and caretaking could have been overlooked. Thirteen female removals produced just one stepmother that began to care for the young after a 5-day interval. If the more frequent male replacements are indicative of an excess of unmated males, one might have expected that females would be the sex with sufficient leverage to demand stepparental investment from their new mates, and yet the only observation of active caretaking runs the other way. Two of Power's stepfathers (plus a third observed after a spontaneous replacement) reared subsequent broods with their new mates later in the same season, suggesting that a risk of divorce after reproductive failure may be the factor deterring infanticide, but direct evidence on Question 7 is lacking.

Western bluebirds (*Sialia mexicana*)

In a study of chick feeding rules, Dickinson and Weathers (1999) found no infanticide by nine western bluebird stepfathers that replaced fathers removed after clutch completion. Two fed the chicks, but not as much as fathers normally do. Steppaternal tolerance in this species is puzzling, because lifetimes are not especially long (Question 4) and female western bluebirds produce replacement clutches (Question 5). Reproductive benefits accruing later in the same season are possible, because western bluebirds sometimes raise two broods per year (Dickinson et al. 1996), but only one of Dickinson and Weathers's nine stepfathers received this payoff. The authors did not address the effect of reproductive failure on within-season divorce (Question 7), but given the rarity of second broods, such divorce seems unlikely to be an important selective force against infanticide.

Because birds are seasonal breeders, benefits of infanticide accrue primarily within seasons (unless infanticide helps maintain a new mate's reproductive value in the longer term, a hypothetical benefit that is nowhere documented). However, the costs of infanticide may often extend across seasons. If we assume that infanticide is maladaptive because of cross-season costs (Questions 4 and 7), then it would seem that the replacement males should have fed their stepoffspring to maintain the pair

bond for the following year. In fact, the rate of divorce between seasons for newly formed pairs was unusually high (up to 50%) compared to the natural rate of 6%, suggesting that the lack of care by stepfathers dramatically increased the likelihood of divorce. Perhaps the territory is a more important reproductive resource than the particular female, and tolerance helps the new male gain the territory. This case clearly deserves further analysis.

Eastern bluebirds (*Sialia sialis*)

Meek and Robertson (1991, 1992) make a convincing case that tolerance should be viewed as mating effort in eastern bluebirds. Seventeen of 25 males removed in the early nestling stage were replaced, and all 17 stepfathers tolerated their predecessors' young; five actually helped feed them, albeit at low levels. Because eastern bluebirds will renest after early season failures, infanticide might have been expected (Question 5); however, high rates of divorce and rearing follow failures within seasons (Question 7) (Pinkowski 1977; Gowaty in Rohwer 1986). Such within-season divorce was not observed by Meek and Robertson (1992), but they point out that their nest boxes were well protected from predators.

Some tolerant stepfathers benefited later in the season by siring their new mates' second broods. None of eight females without replacements raised a second brood, but 27% of the experimental females that attracted replacements did, a figure similar to the rate for controls. If infanticide would have led to a high risk of divorce (Pinkowski 1977; Gowaty in Rohwer 1986), then tolerance or care might yield more offspring than infanticide.

In earlier removal experiments elsewhere in the species' range, Gowaty (1983) did not observe replacements, and widowing had no detectable effect on females' abilities to raise their young. Gowaty (personal communication) has evidence that the extent to which female bluebirds need male help to raise their young varies geographically, and one might expect the behavior of males courting such females to vary accordingly.

White-throated sparrows (*Zonotrichia albicollis*)

In a short-term removal experiment addressing issues of male parental care, 10 white-throated males briefly replaced original territory owners 6 or 7 days after hatching (Whillans and Falls 1990). All sang, followed the female closely, and had clearly discovered the nest, but none was infanticidal. Only one stepfather may have fed the chicks. The original territory males were returned to the study site after these brief removals, and no further monitoring of behavior was reported. Thus, white-throated sparrows appear to tolerate stepoffspring, but most of the crucial questions allowing interpretation of this behavior have not been addressed.

Seaside sparrows (*Ammospiza maritima*)

Greenlaw and Post (1985) removed 33 territorial males, all of which were replaced by adjacent males that enlarged their territories and thereby became bigamous.

Greenlaw and Post reported no instances of infanticide. None of the stepfathers was seen to feed nestlings nor to mob observers who approached the nests. It thus appears that seaside sparrow stepfathers tolerate the young, but do not actively invest in them, although this result might be overturned if replacement males that had no primary mates were observed.

Savannah sparrows (*Passerculus sandwichensis*)

Weatherhead and Robertson (1980) removed eight males immediately after their eggs hatched. Six were replaced (and in one case the second male also was removed and replaced). Six of seven stepfathers made persistent alarm calls when an observer approached the nest, and at least one apparently fed the young. However, Freeman-Gallant (1998) removed 15 males when they had young, with results like those of the seaside sparrow experiment of Greenlaw and Post (1985): all were eventually replaced by neighbors expanding their territories and none of these bigamists fed the young. Weatherhead's population was single brooded, and the limited care observed may have been low-cost mating effort with long-term payoff. Freeman-Gallant's population was double brooded.

Polygynous icterines

For polygynous species we must also ask how stepparental behavior affects the acquisition of future mates. In two removal experiments involving male yellow-headed blackbirds (*Xanthocephalus xanthocephalus*), none of 39 replacing males exposed to completed clutches was infanticidal (Gori et al. 1996; Rutberg and Rohwer 1980). Yellow-headed blackbird females often divorce and disperse before renesting following nest failures (Question 7), but this does not necessarily imply any advantage of tolerance over infanticide, at least in the short term, because females never raise two broods in one season (Gori et al. 1996; Willson 1966). It could favor tolerance in the long term if females whose young are tolerated by a stepfather mate with the same male in future years, but data on this issue are lacking. An additional factor that clearly favors tolerance over infanticide is that females or their nests strongly attract additional females to the territory (Gori et al. 1996). Thus, tolerance by stepfathers seems to function as mating effort directed at other females in this species (Question 8).

The same may be true for red-winged blackbirds (*Agelaius phoeniceus*), but the evidence is weaker. Beletsky and Orians (1991) found that divorce and dispersal prior to renesting within seasons are rare, suggesting that infanticide might be adaptive (Question 7), and yet none of 15 replacement males in the experiment by Rohwer (1985) was infanticidal. However, there is reason to doubt that nests or females on a male's territory have the positive value for attracting future mates in this species that they have in yellow-headed blackbirds. Pribil and Picman (1996) found that female red-winged blackbirds preferred to settle with bachelors, and Searcy (1988) found no preference. There may be geographic variation in these matters (as there is in the degree to which males provision young at all), and even if nesting females are posi-

tive attractants in some populations, the impact of additional females (“harem size”) is unlikely to be monotonic.

OVERVIEW OF EXPERIMENTAL STUDIES

It may seem ironic that we now have stronger evidence that infanticide functions as mating effort (Table 3) than that stepparental tolerance and care do so (Table 4), but this is unsurprising for three reasons. First, stepparental infanticide confirms the assumption that stepparents distinguish their own from other offspring, whereas care or tolerance just raises this as an issue that must be addressed. Second, good data on divorce after reproductive failure are essential to studies of tolerance and care, and collecting such data requires extensive field work and careful analysis (Jackson and Rohwer 1989; Rohwer 1986). Finally, showing that stepparental infanticide functions as mating effort seldom requires assessment of benefits that accrue only over long periods of time, but such effects may be essential for documenting that stepparental tolerance or care in long-lived species represents mating effort that pays off in future breeding opportunities.

Recognizing these complications inspires admiration for efforts to assess the adaptive significance of stepparental tolerance or care (Gori et al. 1996; Martin 1989; Meek and Robertson 1992). But studies of infanticide also have much to offer: those that address constraints on divorce, document the frequency of rapid breeding after reproductive failure, and reveal counterstrategies by the biological parent will contribute strongly to developing an integrated theory of stepparental behavior (Huck 1984; Pusey and Packer 1994; Robertson 1990; Veiga 1993). It is worth noting that only two of the experimental studies of tolerance or care by stepparents that we have discussed were designed to elucidate the puzzling absence of infanticide (Gori et al. 1986; Meek and Robertson 1992); all others were designed as studies of male parental investment or its effects, or as studies of infanticide. Only the study by Martin (1989) of the behavior of willow Ptarmigan stepfathers addresses most of the questions listed in Table 2.

WHAT IS THE ROLE OF CONSTRAINTS?

The evolution of stepparental strategies that might otherwise be adaptive may encounter various sorts of constraints. In the spider *Stegodyphus lineatus*, an unusual constraint appears to preclude any steppaternal strategy other than infanticide: females are eaten by their young, so there is no possibility that a male who tolerates or cares for a female’s eggs or hatchlings will get to mate with her subsequently (Schneider and Lubin 1997). The only issues are whether a female who loses her eggs will breed again, and, if so, whether she will mate with the infanticidal male. The answers are “yes” and “yes.” Females staunchly defend their eggs against males, but when males can overcome these defenses they commit infanticide.

In birds, some cases of stepparental tolerance may reflect handling constraints. A stepparent that might benefit from ejecting a new mate’s unhatched eggs will be

unable to do so unless able either to puncture the eggs or to remove them intact. We cannot imagine that American kestrels, with their small gapes and short hooked bills, could either grasp or puncture kestrel eggs to remove them from nesting cavities, so infanticide may not be an option. This may be why several new pairs abandoned their territories. By removing the failed clutches of the females whose mates had been removed, Bowman and Bird (1987) showed that newly formed pairs could renest.

Apart from kestrels, only the bluebirds listed in Table 4 seem likely to be constrained in their ability to remove eggs. Rohwer and Spaw (1988) developed criteria for assessing the likelihood that host species are able to grasp-eject the eggs of brood parasites. Bill measurements assessed by these criteria indicate that bluebirds could not remove bluebird eggs from their cavity nests without spiking them (Rohwer, unpublished). Replacements could, however, wait for the eggs to hatch, and then throw out the nestlings (see later). Furthermore, divorce following reproductive failure seems to oppose infanticide in eastern bluebirds. For these reasons, we doubt that constraints on their ability to grasp-eject eggs fully explains stepparental tolerance or care seen in bluebirds.

Stronger evidence for constraints on egg handling comes from the timing of stepparental infanticide in barn and tree swallows (Crook and Shields 1985; Robertson 1990). Males that paired with widowed females during incubation tended the eggs until they hatched, and only then did infanticidal stepfathers remove the young from the nest. Furthermore, every case of infanticide reported for both barn and tree swallows involved very young nestlings (Chek and Robertson 1991; Crook and Shields 1985; Møller 1988a; Robertson 1990). Unless birds have sharp beaks, spiked eggs tend to leak into the nest (Rohwer et al. 1989), and it is possible that tree and barn swallows tolerate the delay imposed by waiting for the eggs to hatch because they simply cannot remove eggs from a nest without soiling it (Smith et al. 1996). The fact that tree swallows reline nests containing dead eggs or young, simply covering the dead offspring, argues against this hypothesis (Robertson 1990), but it is supported by the manner by which cliff swallows successfully remove eggs from nests. Because their nests are gently sloped, they roll eggs to the nest entrance, and then either flip them out or spike them at the entrance and carry them away (Brown and Brown 1996). Because the nests of barn and tree swallows are steep-sided compared to those of cliff swallows, rolling eggs to the edge of the nest is impossible for these species, and their bills are poorly suited for cleanly spiking eggs.

HOW MIGHT THE THREAT OF DIVORCE PREVENT INFANTICIDE?

Two crucial questions regarding stepparental tolerance and caregiving, particularly in long-lived species, remain unresolved:

- Is the threat of divorce the primary factor preventing infanticide in species in which newly formed pairs are capable of breeding again quickly?

- If divorce occurs in response to infanticide, why does it occur?

There is a strong observer bias against experimental interventions in studies of long-lived species that form long-term pair bonds. Unfortunately, these are precisely the species for which stepparental tolerance or adoption is likely to constitute mating effort with payoffs in future breeding seasons (Rohwer 1986). How better could a stepparent prove its value as a long-term mate than to demonstrate its competence at raising stepoffspring? Few researchers are willing to do removal experiments with such species, which would include raptors, cranes, and primates. Thus, the very species for which care by stepparents is most likely to be adaptive are the least studied.

The shortage of experiments on long-lived birds makes it important that workers assemble well-documented anecdotes for such species. In addition to several raptors (Grubb et al. 1988; Simmons 1992; additional references in Rohwer 1986), at least four stepmother sandhill cranes showed full care of their new mate's dependent chicks (Nesbitt and Wenner 1987), as did one stepfather (S. Liying, personal communication). Because only male sandhill cranes are capable of holding territories and there is a substantial floating population, Nesbitt and Wenner (1987: 9) observe that a stepmother "would most certainly remain paired and breed with this territorial male during next breeding season."

Rohwer (1986) proposed an experiment to determine whether reproductive failure breaks up new pairs, which has yet to be carried out. It could be most easily conducted with birds such as magpies, gulls, raptors, or cranes, in which stepparents may show care but where reproductive failure, especially early in the breeding cycle, leads to rapid reneating—at least by established pairs. Under these circumstances, selection should favor infanticide unless reproductive failure causes newly formed pairs to divorce. The proposed experiment proceeds in two steps. First, mates are removed from some pairs to get replacements. Second, the clutches of both removal and intact pairs are destroyed, mimicking infanticide and allowing us to assess the response. If controls reneat but newly formed pairs divorce, we may infer that the threat of divorce deters infanticide, which would provide a satisfying adaptive explanation for stepparental tolerance and caregiving. However, it also would open a new question: Why is the instigator of divorce willing to incur the costs of finding a new mate and establishing a new pair bond instead of simply breeding with the infanticidal replacement? Long-lived species with long-term bonds often spend considerable time choosing mates, suggesting that the cost of instigating a divorce may be substantial, and it is difficult to imagine how divorce could evolve specifically to deter infanticide, as this would be spiteful.

We can think of three reasons why divorce after infanticide may persist, in spite of its apparent selective disadvantage. First, divorce could be a nonadaptive manifestation of a response to cues that normally indicate an incompatible or incompetent mate (Rohwer 1986). Assessment of a mate's competence and compatibility is crucial to the fitness of individuals forming long-term pair bonds (Rowley 1983), and if reproductive failure is an indication that one has chosen poorly, divorce should be an adaptive response. One consequence could be selection against

“sneaky” infanticide and in favor of killing the young while their genetic parent is watching, so that the new mate will not misinterpret the reproductive failure as a sign of the stepparent’s incompatibility or incompetence. Another implication of this hypothesis is that divorce should follow reproductive failure in first time breeders without mate replacement as well as in the replacement group in the experiment proposed earlier, but should become less probable if the pair has had prior success.

Second, mate replacement may be so easy that instigating a divorce is essentially free of costs for the genetic parent, as is the case in house wrens (Kermott et al. 1991). This suggests that renesting will scarcely be delayed by dispersal and repairing before a nest failure. If this is true, stepparents should exhibit caregiving, tolerance, or infanticide contingent on their assessment of how much it would cost their mate to initiate a divorce. We thus expect caregiving or tolerance to be relatively prevalent when divorce costs the genetic parent little, and infanticide to be more prevalent as the costs of divorce increase. A seasonal decline in the incidence of infanticide in barn swallows (Møller 1988a), which presumably occurs because of its declining utility as renesting prospects shrink, shows that stepparental infanticide is sometimes a flexible response. However, we know of no data evaluating whether the response of early-season stepparents is contingent on the dispersal options available to the genetic parent/new mate.

Finally, and perhaps most importantly, the breaking of new pair bonds after infanticide may not be psychologically equivalent to divorcing a mate after nest failure, but more a matter of terminating a courtship that is still at an early stage. Assessing the quality of a suitor by observing its stepparental behavior could provide especially valuable information for long-lived species that maintain long-term pairbonds, and if this is true then stepparents might sometimes surprise observers by killing still-dependent offspring only after a period of tolerance or investment. In other words, it is conceivable that stepparents sometimes are selected to provide care only long enough to convince the new mate of their parental competence, and then commit infanticide. Circumstances favoring such a stepparental display of parental competence followed by infanticide are likely to be rare, however, for as time passes, offspring become both more valuable to the genetic parent and less costly to the stepparent, and, if reproduction is seasonal, the probability of successfully raising a new brood also declines. Recall, however, that both tree and barn swallow stepfathers tolerate eggs, but then kill the young when they hatch (Møller 1988a; Robertson 1990). This prolonged courtship hypothesis provides an alternative to the hypothesis that the inability of these swallows to handle eggs constrains the evolution of ovicide: their tolerance of eggs could constitute courtship, solidifying the new pairbond. If replacements that arrive in the immediate posthatch period also are initially solicitous, this hypothesis would be supported, but if they commit infanticide promptly, then the constraint hypothesis of ovicidal inability probably is correct.

The idea that stepparental care is a courtship display may explain why infanticide is not more common in long-lived species in which established pairs readily renest after failure. Because long-lived species that also form long-term pairbonds can expect many future years of breeding, this “courtship phase” of stepparenting

could easily involve the entire period of offspring dependency. Again, the fundamental prediction from the critical experiment of Rohwer (1986), summarized earlier, is that infanticide would result in the breaking of new, but not long-established, pair bonds.

CONTRASTING INFANTICIDE AND TOLERANCE OR CARE

The paucity of experimental work on stepparental tolerance or care probably reflects a bias toward assuming any such behavior to be a by-product of adaptations for care by genetic parents. Implicit in this assumption is the notion that stepparenthood has been too rare or inconsequential for selection to have created relevant adaptations. If this is true, then we would expect species characterized by tolerance or care to have lower rates of naturally occurring stepparenthood than species characterized by infanticide. Among the infanticide studies in Table 3, only Freed (1986) reported this information: he found that 4% to 7% of naturally occurring tropical house wren broods acquired a stepparent. From data provided for some other species, we infer natural rates of stepparenthood to be roughly as follows. About 3% of house sparrow (Veiga 1993) and 4% of barn swallow broods (Møller 1988a) acquired a stepfather, and about 2% of little swift broods acquired a stepparent of one sex or the other (Hotta 1994); all of these species exhibit stepparental infanticide. Among the studies in which the dominant stepparental response was tolerance or care, only Gori et al. (1996) reported natural rates of stepparenthood: 9.2% of yellow-headed blackbird territories acquired a stepfather over the course of the entire season. Obviously more data are needed, but these numbers do not support the hypothesis that tolerance is simply a maladaptive response to a rare event. For any species for which we know the behavior of stepparents, publishing data on natural rates of stepparenthood should be a priority. In addition, much more data relevant to this issue could be extracted from monographs on field studies of particular species.

RELEVANCE TO HUMANS

The human species clearly seems to be one of those in which stepparental care and tolerance function as mating effort. Stepparents of both sexes invest a great deal in the rearing of their predecessors' children, and, unlike adoptions of unrelated children, this is clearly not a novelty. The non-Darwinian literature on stepfamily relationships is potentially misleading in this regard. Focusing solely on the most recent trends in the United States, many social scientists have followed Cherlin (1978) in considering stepparenthood to be a "new role" whose ground rules are not yet established. In cross-cultural and historical perspective, however, the contemporary prevalence of stepfamilies is not particularly high (Dupâquier et al. 1981; Daly and Wilson 1994; Lancaster and Kaplan 1999). In fact, the Ache data of Hill and Hurtado (1996), the Hazda data of Marlowe (1999), and the review by Hewlett (1991) all indicate that young children in at least some traditional foraging societies

were substantially more likely to live with stepfathers than children in any modern nation state.

Although human stepparents invest in their predecessors' children, they invest less than genetic parents of similar means (Anderson 1999a, 1999b; Case et al. 1999; Flinn 1988; Lancaster and Kaplan 1999; Marlowe 1999; Zvoch 1999). This is reminiscent of those nonhuman cases in which stepparents exhibit limited caretaking that falls short of the efforts of genetic parents. In no species do we yet know enough about the costs and consequences of parental efforts to begin to address whether such half-hearted care might reflect the workings of a finely tuned adaptation, with expected payoffs that surpass both those of full parental participation and those of taking the opposite tack and ignoring (or killing) the young. We do not suggest that human stepparents adjust their efforts in ways that maximize their expected future progeny even in modern environments; too many stepparents invest when the prospects of future reproduction are negligible for that to be the case. It is plausible, however, that the manifest variability of stepparental affection and investment reflects a modulated response to ancestral cues of the fitness consequences (including indirect fitness, as discussed later) of various courses of action.

People are much more likely to kill their stepchildren than their genetic children, and this difference in risk is especially large for the youngest children, who have the longest prospective dependency and are the most likely to have a direct delaying effect on the next birth (Daly and Wilson 1996, 1998). Nevertheless, infanticide by human stepparents could hardly be a specific adaptation, as it fails too many tests. It is nowhere routine, and there is no evidence that stepfathers (or stepmothers) who kill, even in traditional societies, enjoy a reproductive benefit on average. Neither is there reason to believe that they can kill without risking grave costs, for unlike the situation in most other species, a new mate, even if fully adult, is likely to have concerned relatives. Most telling is the fact that stepparental infanticide seldom is performed efficiently. For every stepparent who kills, there are many more who inflict nonlethal abuse on stepchildren and actually raise their own and their partners' investment costs by so doing (Daly and Wilson 1985).

Human mating and reproduction are unusual in several features that bear on the costs and benefits of stepparental investment. The interests of two potentially large kin groups are involved in both the establishment and the dissolution of a marriage, which means that generous courtship gestures such as stepparenting may function not only as mating effort but also as alliance building. The kin universe surrounding a married couple also is likely to afford deterrence of extreme acts of self-interest such as infanticide, and it means that children who are not welcomed by a stepparent can often be fostered, entirely or in part, to other relatives who have at least some benevolent interest in their welfare. Another peculiarity that must affect the costs and benefits of alternative stepparental responses is that offspring dependency lacks a discrete developmental endpoint, and parents care simultaneously for children of different ages and needs.

The principal lesson of this review for students of the human animal is that investing stepparents are neither peculiar to our species nor beyond adaptationist explanation. Although stepparental infanticide occurs in many diverse taxa, it perhaps

even more often is the case that nonhuman stepparents tolerate and care for their wards. And although many puzzling cases remain to be fully explained, it appears that stepparental tolerance and care are best interpreted as acceptable costs of courtship.

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