

# Defending young biparentally: female risk-taking with and without a male in the burying beetle, *Nicrophorus pustulatus*

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**Abstract** A positive correlation between the parental effort of a male and female should promote stable biparental care. Risk-taking (as assessed by injuries) against infanticidal intruders by *Nicrophorus pustulatus* females was expected to be low when females had a low probability of successful defense of the young. I tested the hypothesis that when the presence of a male partner increased the probability of successful defense from low to moderate that female risk-taking would increase. Single females and pairs with first instar larvae were confronted by potentially infanticidal male and female conspecific intruders. Male intruders routinely took over nests from unpaired females (30 of 36 trials). Unpaired females and male intruders were injured infrequently, indicating less intense fights despite the high probability of infanticide. A resident female defending against a male intruder was injured more often when paired than unpaired, suggesting greater risk-taking. A male parent that delays desertion, therefore, receives fitness benefits not only from his own defense of the young, but from greater female defense against male intruders as well. It is hypothesized that the threat of infanticidal takeovers by males promotes extended biparental care in burying beetles. When the intruder was female, on the other hand, a female parent on her own had a moderate probability of successfully defending the brood (22 of 36 trials). The presence of a male partner against female intruders almost guaranteed successful defense (35 of 36 trials) and female intruders did not appear to contest

pairs vigorously. Against female intruders the presence of a male partner did not significantly change injury rates of the defending female.

**Keywords** Parental care · Brood defense · Infanticide · Parental effort · Cooperation

## Introduction

Parental defensive effort and willingness to take risks, like other contest behavior, will vary with resource-holding potential (Parker 1974) and the relative value of winning a contest by the two contestants (Houston and McNamara 1988). A parent defending against a potentially infanticidal intruder might be expected to take few risks when the probability of a successful outcome is low and defensive effort of the parent is unlikely to alter the outcome (reviews in van Schaik and Janson 2000). Similarly, if the intruder has low resource-holding potential or the reproductive value of committing infanticide is low, then the intruder is not expected to take risks. In both cases, injuries are expected to be infrequent. The greatest escalation of potentially infanticidal encounters and the highest probability of injury are expected when both the parent and intruder place a high value on a successful outcome and both individuals assess that the probability of winning is non-trivial (Palombit 1999; van Schaik and Janson 2000). Our understanding of contests between two individuals (Enquist and Leimar 1987, 1990; Riechert 1998) can be an important starting point to understand the dynamics of biparental defense of the young.

The way that each parent responds to the presence and effort of its partner will affect the parenting system and the success of the brood. Because parental effort exacts costs

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on the individual providing care while benefits accrue to both parents (Lessells 2006), we anticipate conflicts of interest over how much care each provides (Houston et al. 2005; Trivers 1972). Our typical expectation is that greater parental effort by one parent will lead to less effort by its partner (Chase 1980; Houston and Davies 1985).

If, on the other hand, the presence of a second parent can increase the probability of success from low to moderate then risk-taking by the first parent might be expected to increase. In this case, the defensive effort of the two parents would be positively correlated; when the second parent delays desertion and defends it receives fitness benefits not only from its own effort but also from greater defensive effort by its partner. This would be expected to promote a stable biparental association.

The necessary conditions to test this hypothesis are met in burying beetles. Unpaired females or male–female pairs produce broods on a small vertebrate carcass (Eggert and Müller 1997; Müller et al. 2007; Scott 1998a). An infanticidal intruder of either sex might discover the resource and attempt to kill the brood, mate with the opposite-sex resident, and use the resource for a replacement brood (Trumbo 1991; Trumbo and Valletta 2007). Infanticidal takeovers in burying beetles are a regular occurrence in the field (*Nicrophorus orbicollis*, Robertson 1993; Scott 1990; *Nicrophorus vespilloides*, Suzuki 2000) and produce direct genetic benefits for intruders (Trumbo 1990b). Both heterospecifics and conspecifics, and both males and females exhibit infanticide (Koulianos and Schwarz 2000; Suzuki 2000; Trumbo 1990a, 2006; Wilson et al. 1984). Unpaired females are especially vulnerable to a takeover by a conspecific male (*N. orbicollis*, Robertson 1993; Scott 1994; Trumbo 1990b). After the brood reaches the second instar, the value of the resource for an intruder declines rapidly and contests are infrequent (Trumbo and Valletta 2007).

Burying beetles are facultatively biparental with females remaining near the nest until larvae disperse. The male typically leaves earlier, but the timing of male desertion varies with the vulnerability of the brood (*N. orbicollis*, Scott 1998b; Trumbo 1991). The male and female partners recognize each other by a “parental” pattern of cuticular hydrocarbons and will attack any nonparental intruder (*N. vespilloides*, Müller et al. 2003). The added presence of a male reduces the probability of a takeover (*N. orbicollis*, Robertson 1993; Scott and Gladstein 1993; Trumbo and Fiore 1994), but the effect of the male’s behavior on female defense of the brood, critical information for understanding why biparental care is maintained, is not known for any species of *Nicrophorus*.

*Nicrophorus pustulatus* Herschel, the subject of the present study, will breed readily on carcasses or snake eggs in the laboratory (Blouin-Demers and Weatherhead 2000;

Trumbo and Valletta 2007). In the field, *N. pustulatus* is readily trapped at well-rotted carrion on which it feeds but the primary resource for breeding is likely snake eggs (Smith and Trumbo, unpublished data). *Nicrophorus pustulatus* is apparently undergoing a remarkable host shift while retaining the ancestral ability to prepare carcasses for breeding. Despite this host shift, *N. pustulatus* exploiting carrion has a very low rate of brood failure and a high conversion efficiency of resource to offspring compared to other *Nicrophorus* spp. *Nicrophorus pustulatus* is also very aggressive, protecting larvae and contesting for carcasses (Trumbo 2007), making it an amenable subject for testing hypotheses of parental defense of offspring.

In this study, I test the hypothesis that there are competitive interactions where the effort of one parent will be positively correlated with the presence of a second parent; specifically, that a single female with a low probability of preventing a takeover and infanticide against a male intruder will not risk injury defending the brood, but that risk-taking will be higher when she is paired with a male who also defends. I will also show that this positive correlation of male and female effort cannot be explained sufficiently by a third variable such as similar responses to changing brood value (e.g., Carrillo and Aparicio 2001) or to an altered level of threat (e.g., Itzkowitz et al. 2005). Interactions with female intruders were also examined in which the presence of a male partner was expected to increase the probability of successful defense sufficiently that intruders would not vigorously contest for the resource.

## Materials and methods

### General methods

A colony of *N. pustulatus* was established from wild-caught beetles baited with well-rotted carrion in the research forest of Berea College, Kentucky. Experimental subjects were maintained on a 15 L: 9D cycle at  $21 \pm 1^\circ\text{C}$  and fed scraps of chicken liver for 25–35 days before experimental trials. Pronotal width was measured at the widest point with digital calipers. Subjects were isolated in a small container (9 cm diameter) with water the day before a trial. All individuals (residents and intruders) were uninjured at the start of the trial.

Subjects for a particular replicate were of the same age. Mean pronotal size of residents was held equal across treatments because body size is related to competitive ability (Otronen 1988). Pronotal size of an intruder was 5–10% greater than the resident(s) for that particular trial to avoid the possibility that the resident(s) would always win (Trumbo and Valletta 2007). All trials were run in covered plastic containers (30×18×11 cm), 3/5 filled with soil, with

a mouse carcass partially covered by a paper towel. Intruders were introduced on the carcass without handling (direct transfer from an isolating container to breeding container). All carcasses were *Mus musculus* L., frozen shortly after death, and thawed 24 h before experimental trials. Mean carcass mass was equal across treatments.

#### Single females and pairs confronting an intruder

There were four treatments ( $N=36$  per treatment): resident female/male intruder, resident pair/male intruder, resident female/female intruder, and resident pair/female intruder. All trials began with a male–female pair established on a 24- to 29-g carcass. On day 4, trials were checked to determine whether first instar larvae were present. If not, the setup was checked for larvae again on day 5 (two of 144 setups did not have larvae by day 5; these were excluded and replaced with beetles from the colony to maintain the original sample size). Once larvae were present, the male resident was removed in one-half of the trials (single female trials); the nest was similarly disturbed, but no parents were removed in trials with a defending male–female pair. In this way, broods defended by pairs and single females had received equivalent parental care, and would be of equivalent value just before the manipulation.

A male or female intruder was then introduced during their inactive period and covered with soil (the intruder would typically discover the carcass about 6–8 h after experimental removal of the male parent). After 2 days (day 6 when the manipulation occurred on day 4), the setups were checked again to determine whether any larvae were present. The absence of any larvae and the presence of the intruder on the carcass was scored as an infanticidal takeover. The resident(s) and intruder were also checked for injuries on legs and antennae. If larvae from the original brood were present, the resident male (in trials with pairs) and the intruder were removed (the resident male would normally disperse about this time); removal prevents injuries between male and female partners that are confined beyond the normal paternal period. If larvae were not present 2 days after the intruder introduction (evidence of an infanticidal takeover), a defeated resident of the same sex as the intruder was removed. Trials continued until the original or replacement brood dispersed from the carcass. Within 24 h of dispersing, the larvae were counted and weighed.

#### Statistical analysis

Statistical analysis followed SAS (2000). Tests of frequency employed a  $2 \times 2$  contingency table analysis unless small expected cell frequencies indicated Fisher's exact test (all reported values for Fisher's exact test are two-tailed).

Frequency data relating an outcome from an encounter to two experimental variables were analyzed using a  $2 \times 2 \times n$  log-linear analysis. Values for the interaction between experimental variables are reported for frequency tests whether or not the interaction was significant, following Cox and Snell (1989). Two-way analysis of variance (ANOVA) was used to compare the brood size and brood mass after tests for homogeneity of variance.

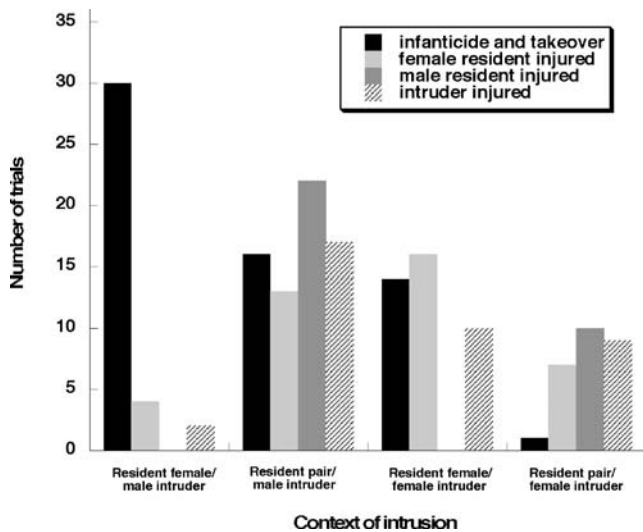
## Results

#### Single females and pairs confronting intruders

When a single female or pair was challenged by a male or female intruder on day 4, the probability of a takeover and complete infanticide of the brood was related both to the number of residents defending and to the sex of the intruder (Fig. 1;  $G^2_{\text{No. of residents}}=21.30$ , 1 *df*,  $P<0.0001$ ,  $G^2_{\text{Sex of intruder}}=28.36$ , 1 *df*,  $P<0.0001$ ,  $G^2_{\text{No. of resident} \times \text{sex of intruder}}=7.42$ , 2 *df*,  $P=0.02$ ,  $2 \times 2 \times 2$  log-linear analysis). When considering only trials involving a resident pair, the male resident was injured more often than the female resident, and injuries to residents were more common when the intruder was male rather than female (Fig. 1;  $G^2_{\text{Sex of resident}}=4.36$ , 1 *df*,  $P=0.04$ ,  $G^2_{\text{Sex of intruder}}=9.90$ , 1 *df*,  $P=0.002$ ,  $G^2_{\text{Sex of resident} \times \text{sex of intruder}}=0.88$ , 2 *df*,  $P=0.94$ ,  $2 \times 2 \times 2$  log-linear analysis).

The results indicate that males may be more competitive as intruders (Trumbo 2006) and may be more willing to risk injury as parents. The behavior of the female parent appears to be more context specific. When defending against a male intruder, a female was more likely to be injured when paired with a male than when alone (Fig. 1;  $P=0.025$ , Fisher's exact test). The higher injury rate when paired occurred even though her brood was at less risk than when she defended alone. The relative risk of injury to the resident female when paired versus alone was 3.25 (1.26–8.57, 95% CL) when confronting a male intruder. The lower intensity of conflict between a single female resident and male intruder was also indicated by a much lower frequency of injuries to male intruders when facing single females rather than pairs ( $P<0.001$ , Fisher's exact test).

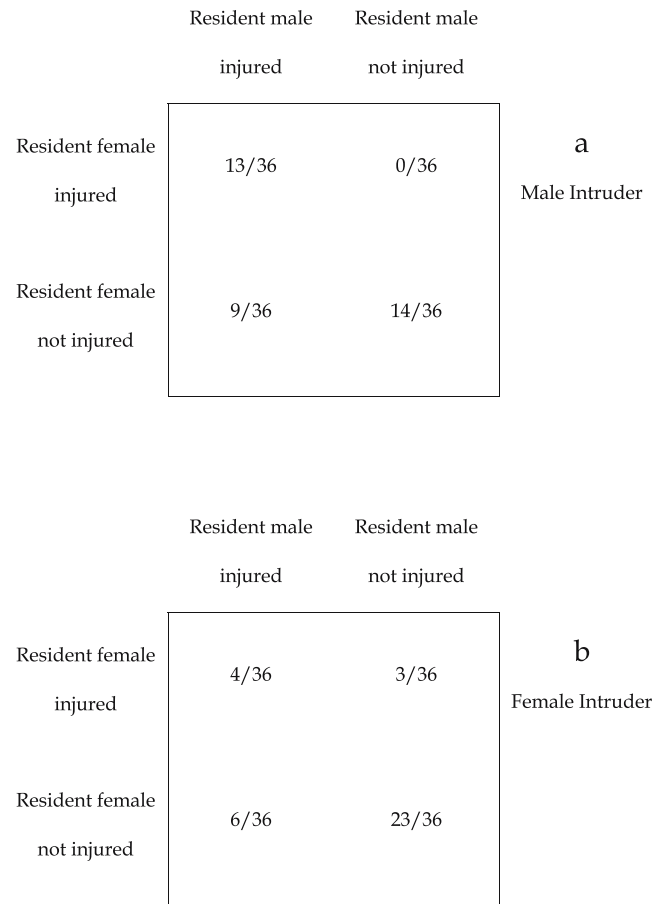
A low rate of injury for defending parents may be due to either limited risk-taking by parents or to intruders that do not vigorously attempt to take over resources and commit infanticide. It is therefore revealing to examine injuries in only the subset of trials in which a takeover and infanticide occurred. When pairs defended against either male or female intruders, or when single females defended against female intruders, at least one resident was injured in 30 of 31 (96.8%) trials in which a takeover occurred. In these three contexts, it is almost certain that the intruder will have to fight intensely and injure a resident for the opportunity to



**Fig. 1** The number of trials (out of 36) in which a takeover and infanticide occurred, and the frequency of injuries, when single females and pairs were challenged by an intruder

use the resource for reproduction. The one context in which an infanticidal takeover occurred and yet the parent was infrequently injured was when males intruded on single females. In this context, only three of 30 (10%) single female parents were injured, significantly less often than in other contexts ( $P < 0.001$ , Fisher’s exact test). When a male–female pair defended against a male intruder, there were nine trials in which only one parent was injured. This would be expected to be more often the male parent as 62.9% of injuries to defending pairs were on males. Taking account of the higher injury rate on males, it is still unlikely that by chance all nine cases of injury on just one parent would be on the male ( $P = 0.02$ , Binomial test; Fig. 2a). The male parent has more to lose in this context. If a male intruder takes over the carcass, the resident male will achieve almost no reproductive success. The female parent, however, has the opportunity to pair with the intruder and to produce a replacement brood. When the intruder was male, it was clear that females did not take risks unless her partner took risks. In all 13 trials in which the female was injured, the male parent was also injured (Fig. 2a). When the intruder was a female, there were three trials in which the female parent was the sole parent injured (Fig. 2b).

Although the presence of a male parent decreased takeovers, there was no effect of the male on brood production in trials in which a takeover did not occur. Both brood size and total mass of the brood were significantly related to the sex of the intruder (brood size:  $F_{1,80} = 4.11$ ,  $P = 0.05$ ; brood mass:  $F_{1,80} = 12.69$ ,  $P < 0.001$ ; Fig. 3), but not to whether a single female or pair cared for the brood (brood size:  $F_{1,80} = 0.52$ ,  $P = 0.47$ ; brood mass:  $F_{1,80} = 0.002$ ,  $P = 0.96$ , two-way ANOVAs). The finding that brood production was smaller when successfully defending against a female rather than a



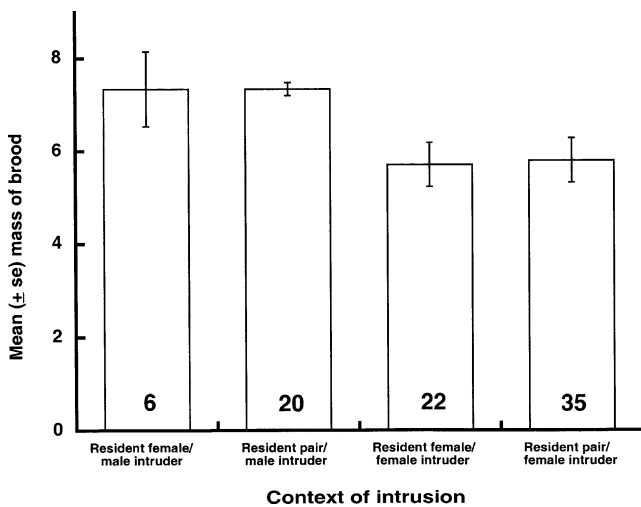
**Fig. 2** The number of injuries (out of 36) to male and female residents in pairs when challenged by a male (a) or a female (b) intruder

male intruder is consistent with an earlier study demonstrating greater interference by defeated female intruders than by defeated male intruders (Trumbo and Valletta 2007).

**Discussion**

The hypotheses that single females with a low probability of preventing infanticide should take few risks, and that the presence of a defending male would increase female risk-taking were supported in the context of male intruders. The susceptibility of unpaired females of *Nicrophorus* to takeovers by males has been shown to be ecologically important in the field in *N. orbicollis* (Robertson 1993; Trumbo 1990b) and is likely the most common context for a takeover. The female has an important incentive to deter takeovers by male intruders when successful defense is possible. A replacement brood after infanticide of first instars by a male intruder will be approximately one-half the size of her original brood (Trumbo and Valletta 2007).





**Fig. 3** The mean ( $\pm$  SE) brood mass produced by successful single females and pairs that prevented takeovers when challenged by a male or female intruder (sample sizes are at the base of the bars)

The behavioral response of the female to an intruder should influence male desertion behavior.

A male that stays and provides care receives fitness benefits not only from his own care, but also from greater female effort against male intruders. A positive correlation of female effort and male presence is hypothesized to promote extended, biparental care.

Beyond the nest initiation phase, a positive correlation of effort between the two parents is typically only expected when the effort of both parents is correlated with a third variable. For example, both parents may expend more effort in defense as the value of the brood increases with age (Carrillo and Aparicio 2001). Brood value was controlled in the present study by keeping all females paired until shortly before the introduction of the intruder. Broods from both the single female and paired treatments had received similar levels of parental care and were of similar value at the time of the experimental manipulation, and again at the time larvae dispersed from the nest in trials in which the intruder was repelled (Fig. 3). A positive correlation of defensive effort may also result when the effort of both parents increase together in response to an increasing threat, or decrease together to a decreasing threat (Itzkowitz et al. 2005; Taborsky and Foerster 2004).

In the present study the threat level (male or female intruder) was controlled across the single female and pair treatments, and all intruder introductions occurred at the same stage of larval development. A low level of threat cannot explain infrequent injuries to single females defending against a male intruder. When defending against males, females were injured less often when defending alone and the brood was most at risk (83.3% takeovers), and injured more often when the male partner was present and the brood was less at risk (44.4% takeovers). When the intruder

was male, increased female risk-taking was related to the presence of a male partner, not to a greater threat or higher brood value.

Female parents were not injured more frequently when paired if the intruder was female. Even without the help of a male, a defending female had a moderately high probability of preventing a takeover (22 of 36 trials). The low incidence of injuries to pairs defending against a female intruder likely reflects the low threat that female intruders presented to pairs (only one takeover in 36 trials). Pairs had three important contest asymmetries in their favor against female intruders: two competitors versus one, the intruder was of the less competitive sex (Trumbo 2006), and the original brood had nearly three times the value of a replacement brood by a female intruder (Trumbo and Valletta 2007). In the majority of these trials (Fig. 2b), no beetle (resident female, resident male, intruder female) was injured. Residents were certainly ready to take risks against female intruders. In the one trial in which a takeover occurred, both the male and female parents were injured; in 13 of 14 trials in which a female took over a nest from a single female, the resident female was injured.

In general, we expect a negative correlation of effort by the male and female parent (Dawkins and Carlisle 1976; Houston et al. 2005; Trivers 1972; Westneat and Sargent 1996), which is just one aspect of sexual conflict between unrelated males and females (Arnqvist and Rowe 2005). Conflict over care is accentuated with diminishing benefits for increasing parental effort (Ratnieks 1996), incorporated into almost all our models of biparental care (Chase 1980; Houston and Davies 1985; McNamara et al. 1999; Winkler 1987). A competitive situation represents a discrete event for which a threshold may have to be reached for benefits to accrue (Trivers 1972). Parents should be sensitive to situations in which one parent cannot meet the threshold. The penalty for underinvesting can be far more severe for a threshold model of parental effort as opposed to models incorporating diminishing benefits.

McNamara et al. (2003) noted that with diminishing benefits, a parent may be selected to withhold care even if benefits from the next increment of care exceed costs, if such effort makes it more likely that the partner will desert or withhold care. When a threshold must be reached to produce benefits, conversely, a parent may be selected to provide care even if costs from the next increment of care exceeds benefits, if such effort makes it more likely that the partner will continue care.

The effect of group size on both the probability of winning contests and the motivation to defend the young need to be incorporated into studies of parental care. It should not be surprising that in social groups, the critical number of individuals participating in group-beneficial behavior can have profound effects on the behavior of

other group members (Valencia et al. 2006). In burying beetles, it is likely that the greater success of pairs against male intruders is a consequence of a synergism resulting not only from having two defenders, but from having at least one parent more motivated as well. Analyses of models of contests in nonparental situations suggest that an individual with a low probability of winning may not compete intensely, despite a high value for a contested resource (Enquist and Leimar 1983). Primates may represent a very different system in which the motivation to defend young may depend on the presence of others willing to defend. Female primates that are unaided may not confront a potentially infanticidal male and are rarely injured in such situations.

Defense may be more active if there is support from other females or a male partner (see reviews in van Schaik 2004; van Schaik and Janson 2000). The threat of infanticide has been proposed as a selective force for group behavior (Sterck et al. 1997; Wrangham 1979) and monogamy (Palombit 1999; reviews in van Schaik 2004; van Schaik and Janson 2000). For logistical and ethical reasons, it is difficult to perform controlled experiments on infanticide in these groups. Among social insects, cooperation in competitive situations is thought to be a strong binding force favoring the evolution of group behavior. Even in incipient social groups, one task where the effectiveness per capita may be higher in groups than for solitary individuals is defense (Hölldobler and Wilson 2005).

Parental care in burying beetles is complex, not only because it takes many forms but because of the mixture of binding and dissolutive forces affecting the biparental association. There are known conflicts over feeding the young (Fetherston et al. 1994; Rauter and Moore 2004; Smiseth et al. 2005); despite male participation in feeding young, his presence does not increase the brood size or brood mass in the absence of intruders (Jenkins et al. 2000; Sakaluk et al. 1998; Scott and Gladstein 1993; Smiseth et al. 2005; Trumbo and Fernandez 1995, this study). Increased female risk-taking in the presence of a male partner in high-threat contexts may help to counter the dissolutive forces destabilizing biparental care in burying beetles. This is not to say that there are no potential conflicts over defense as well. We might expect conflict when the effort of one parent can easily exceed a competitive threshold.

Given that a burying beetle with a brood intensely attacks a same-sex intruder, the behavior of the partner should be more nuanced. Important selective factors are expected to be the relative value of the original brood compared to a replacement brood for a resident that can pair with the intruder, the difference in effectiveness of two parents versus one, and the abilities of the male and female parents to defend. Although conflicts over care exist for

parental care in burying beetles, sexual conflict within the biparental group may be moderated in a high-threat context when the presence of a second parent increases the parental motivation of its partner.

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This research complies with current federal, state, and local law.

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