

# Effects of body size on investment in individual broods by male pine engravers (Coleoptera: Scolytidae)

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**Abstract:** Large body size is generally associated with mating advantages and greater vigour in insects and other animals. Greater mating opportunities may favour reduced investment in individual broods, but greater vigour may contribute to greater brood success. To consider these issues, we examined the effect of body size of male pine engraver beetles, *Ips pini* (Coleoptera: Scolytidae), on the duration of paternal care and the reproductive success of their individual broods in a laboratory experiment. Larger males abandoned their mates and brood earlier than did small males. Nevertheless, larger males had more offspring and, when offspring emergence date was controlled by focusing on early emergers, larger males had larger offspring. There was no detectable effect of male size on the breeding behaviour of their mates. This study indicates that larger individuals realize higher fitness both through increased mating opportunities and through greater reproductive success in individual broods.

**Résumé :** Il est généralement admis qu'une grande taille offre des avantages au moment de la reproduction et est synonyme d'une plus grande vigueur chez les insectes et les autres animaux. La probabilité plus élevée de s'accoupler peut favoriser la réduction des couvées chez les individus, mais une plus grande vigueur est souvent associée au succès plus grand de la progéniture. Pour éprouver ces hypothèses, nous avons examiné l'effet de la taille des mâles sur la durée des soins paternels et sur le succès reproducteur des diverses couvées au cours d'expériences en laboratoire sur des Scolytes du pin, *Ips pini* (Coleoptera : Scolytidae). Les mâles les plus gros abandonnent leur partenaire et la couvée plus tôt que les mâles plus petits. Néanmoins, les mâles plus gros produisent des couvées plus nombreuses et, en éliminant l'effet de la date d'émergence, ne tenant compte que des premiers individus émergés, on constate que les mâles plus gros ont des rejetons plus gros. Nous n'avons pas constaté d'effet décelable de la taille des mâles sur le comportement reproducteur de leurs partenaires. Cette étude permet d'affirmer que les individus plus gros ont de façon générale un meilleur fitness grâce à leur probabilité plus grande de s'accoupler et au succès reproducteur plus élevé de leur progéniture. [Traduit par la Rédaction]

## Introduction

Organisms face a fundamental trade-off between investing in current and future reproduction (Trivers 1972; Reznick 1985). Consequently, the optimal amount of investment in a particular brood or mating attempt is expected to depend on the prospects for obtaining additional matings (Maynard Smith 1977). As predicted, several studies have shown that investment in individual mating attempts or broods is reduced when mating opportunities are increased (e.g., Keenleyside 1983; Burley 1986; McLain 1989; Carroll 1991).

Body size is an important life-history character that is often positively correlated with an individual's mating opportunities (Roff 1992), as has been particularly well documented for insects (Thornhill and Alcock 1983; Roff 1992).

Consequently, larger individuals may be more prone to desert a current brood because the prospects of breeding again elsewhere are high, an idea that we refer to as the mating opportunities hypothesis. On the other hand, the advantages of large body size that enhance survival and dispersal may also allow greater investment in individual broods (Winkler 1987; Reiss 1989), an idea that we call the general vigour hypothesis. These hypotheses may not be mutually exclusive. For example, high-quality individuals may be able to invest more in absolute terms in an individual brood but still expend a smaller proportion of their reproductive budget in the brood than could low-quality individuals.

Here we examine the effects of male body size on the duration of paternal care and on reproductive outcome in individual broods of pine engraver bark beetles, *Ips pini* (Say) (Coleoptera: Scolytidae). Male pine engravers establish nuptial chambers under tree bark and within a few days they attract several females who alone construct egg galleries radiating from the chamber. Males then remain with their mates and brood for several weeks (Schenk and Benjamin 1969). During this residence time, males keep egg galleries clear of frass, enhance their mates' oviposition rates, and defend the gallery system against offspring predators, but

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they do not attract additional mates (Reid and Roitberg 1994). After this reproductive bout, when habitat quality has degraded, parental pine engravers reemerge from their galleries and disperse in search of other breeding opportunities.

As with other insects, larger body size in bark beetles appears to confer greater breeding opportunities. Among various species of bark beetles, larger individuals have higher survivorship (Cole 1973; Safranyik 1976; Gries 1985; Langor and Raske 1987) and greater dispersal ability (Thompson and Bennett 1971; Gries 1985), tend to be the first to colonize breeding sites when habitat quality is highest (M.L. Reid, unpublished data), and produce more sex pheromone than smaller males (Anderbrant et al. 1985). Female pine engravers appear to prefer larger males (Reid 1992), although there is no clear evidence of assortative mating with respect to body size or greater mating success of large males in natural populations of bark beetles. While large body size clearly increases breeding opportunities, the effects of male body size on paternal care in bark beetles are unknown. Therefore we conducted a laboratory rearing experiment in which we varied male body size to determine its effect on the duration of care and on reproductive success in individual broods.

## Methods

Pine engravers were obtained from lodgepole pine, *Pinus contorta* var. *latifolia* Engelman, which had been naturally colonized by overwintered adults near Princeton, British Columbia, Canada. Colonized logs were placed in large screened cages at 28°C. Emerged beetles were collected daily, placed in jars with tissue paper, and kept at 4°C until needed (for a maximum of 2 weeks).

To index beetle body size, we measured pronotum width and total body length (anterior edge of the pronotum to the posterior edge of the elytra) using a stereomicroscope fitted with an ocular micrometer at 25× magnification. Measurements were precise to the nearest 0.04 mm. We also calculated body volume for each beetle on the basis of their cylindrical shape ( $\pi \times (\text{width}/2)^2 \times \text{length}$ ). To ensure a broad representation of male body sizes in our sample, we chose equal numbers of males (14) from three size categories based on pronotal width: small ( $\leq 1.48$  mm), medium ( $> 1.48 - 1.60$  mm), and large ( $\geq 1.60$  mm). Small and large males deviated from the mean male size for most of the collections we have made over several years by at least 1 standard deviation. Mean ( $\pm$ SD) pronotum width was  $1.54 \pm 0.069$  mm, body length  $3.92 \pm 0.202$  mm, and body volume  $7.35 \pm 0.969$  mm<sup>3</sup>. To minimize the effects of female body size, females at the extremes of the size distribution were excluded. The mean pronotum width of the females used in the experiment was 1.52 mm (SD = 0.069 mm, range 1.36–1.72 mm).

All parental beetles were marked so that we could monitor the initiation of breeding and recognize reemerging parents. The mark was a small spot of Superglue<sup>®</sup> placed at the edge of the elytral declivity, to which fluorescent powder was added. These marks were not always permanent, so only a subset of reemerged beetles could be detected (the rest were indistinguishable from adult offspring). A preliminary study revealed no detectable effect of marking on mortality.

Each experimental male was placed on a separate lodgepole pine log, provided with three females, and allowed to breed. Logs were 13–15 cm in diameter and 30 cm long. They were cut from three recently felled trees near Princeton, and their ends were sealed with hot paraffin within a day of cutting to prevent desiccation. To establish the male's nuptial chamber in the bark at the centre of a log's long axis (to allow symmetrical room for radiating egg galleries), males were "implanted" by confining them within half a gel capsule over a premade small hole. Before implantation, beetles were kept at room temperature for 24 h to ensure that they were ready to initiate breeding. Successful implantation was indicated by the production of copious frass and boring dust. On each successive day after a male was implanted, a single female was added to the gel capsule, up to a total of three females per male. This number and rate of female introduction match the natural breeding arrangement for an individual male (Swaby and Rudinsky 1976; Reid and Roitberg 1994). Females were assigned to males arbitrarily (without regard to female size). Mean female size per male did not differ among the three male size categories for pronotum width (ANOVA:  $F = 0.199$ ,  $p > 0.8$ ). Some males and females died, did not enter the nuptial chamber, or escaped from the gel capsule after 24 h; these were replaced until a full complement of one male and three females was obtained (except for two cases in which there were only two females and one in which there was only one female).

Logs with the implanted males and females were placed in individual screened cages that were arranged on seven shelves in rows of six (42 cages). Most cages (35 of 42) were 20 cm high, 30 cm wide, and 60 cm long, while the remaining 7 cages were 20 × 40 × 90 cm; we detected no effect of cage type in all analyses. At one end of each cage an opaque white plastic funnel was mounted on plywood and a transparent collecting vial was placed on the end of the funnel's spout. This end of the cages faced a bank of fluorescent lights (six 120-cm tubes, 40 W each) that was the room's only light source (18 h light : 6 h dark photoperiod). Newly emerged beetles are phototactic, and they moved from the log through the funnel into the collecting vials. The mean temperature was 26.7°C (range 21–33°C), with 55% relative humidity.

To ensure that males were evenly distributed with respect to body size in the array of cages, we assigned males to cages according to a stratified random design. We arranged cages as four adjoining replicates of a 3 × 3 Latin square design (plus one row) so that cages for a given pronotum width category were separated vertically and horizontally by cages for each of the other two size categories. Males within each pronotum width category were then assigned randomly to cages so designated.

From 6 July to 6 October, we gathered beetles daily from the collecting vials on each cage. We also examined each log twice a week for any secondary gallery initiations by reemerged parents or emerged offspring. We exposed all secondary galleries, measured their lengths, collected adults, and destroyed visible eggs or larvae to ensure that emerged offspring were from the galleries we established. To determine the original emergence–reemergence dates of beetles in secondary galleries, we estimated 1 day for every centimetre of gallery (Schenk and Benjamin 1969). For single males in secondary nuptial chambers, we assumed that emer-

gence had happened 2 days before discovery. We examined all collected beetles for fluorescent marks and measured their pronotal width and total length.

## Results

The three measures of body size (pronotum width, total length, and volume) were highly correlated with each other ( $p \ll 0.001$ ). Henceforth we use body length as our measure of body size, because it is a larger measurement more appropriate to the level of measurement precision.

### Gallery establishment

Of the original cohort of 42 experimental males, 22 successfully initiated a nuptial chamber within a day. Of the remainder, 9 escaped, 7 died, 2 did not dig, and 2 had unrecorded reasons for failure. There was no difference in body size among successful, escaped, and dead males (ANOVA:  $F = 0.18$ ,  $N = 42$ ,  $p > 0.8$ ).

We examined the first cohort of females provided to males to determine whether successful entry of the female into the male's nuptial chamber depended on male or female characteristics (second and third cohorts faced more variable gallery conditions and were not considered for this analysis). Of the first cohort of females, 26 successfully joined the male in his nuptial chamber. Of the remaining females, 4 escaped, 3 died, 6 began digging their own entrance (and were replaced), and 3 were alive but had not entered the nuptial chamber after 1 day. There were no detectable differences in outcome among male body sizes ( $F = 0.39$ ,  $p > 0.8$ ), female body sizes ( $F = 1.52$ ,  $p > 0.2$ ), and no difference between male and female body sizes ( $F = 1.13$ ,  $p > 0.3$ ).

Seven of the 42 cages failed to produce any offspring, for unknown reasons. Male body size did not differ between successful and failed galleries ( $p > 0.7$ ). These cages are excluded from subsequent analyses.

### Parental residence time

Twelve marked males and 24 marked females were recovered after reemergence. The remaining parents either lost their marks or died in the galleries. Males that were recovered did not differ in body size from nonrecovered males ( $t = 0.97$ ,  $N = 35$ ,  $p = 0.34$ ). Of the recovered marked males, larger males abandoned their galleries significantly earlier than did smaller males (Fig. 1a;  $r = -0.646$ ,  $N = 11$ ,  $p = 0.032$ ; one male with a single mate was excluded from this analysis). Recovery of maternal females did not depend on the body size of their mates ( $t = 0.93$ ,  $p = 0.36$ ). For recovered maternal females, residence time did not vary detectably with either her or her mate's size (multiple regression,  $p > 0.7$ ; effect of female size:  $F = 0.65$ ,  $p > 0.4$ ; effect of male size:  $F = 0.06$ ,  $p > 0.8$ ).

### Offspring number

Larger males produced significantly more offspring than did smaller males (Fig. 1b;  $r = 0.522$ ,  $p = 0.002$ ,  $N = 32$ , for ln-transformed offspring number). There was no effect of paternal body size on offspring sex ratio (defined as the proportion of females;  $r = 0.114$ ,  $p = 0.54$ ). The positive effect of large male size on offspring number was also evident for the subsample of marked reemerged males. When

offspring number was regressed on both paternal body size and residence time simultaneously, only paternal body size was significant (body size:  $F = 12.15$ ,  $p = 0.008$ ; residence time:  $F = 0.05$ ,  $p = 0.827$ ;  $N = 11$ ). Thus, larger males produced more offspring despite leaving their galleries earlier.

### Timing of offspring emergence

To examine the effect of paternal body size on the timing of offspring emergence, we used two measures of emergence time: the median emergence date for each cage and the mean emergence date of the sixth to tenth offspring of each sex. We considered female and male offspring separately because females emerged, on average, 6.5 days ( $\pm 2.26$  days) before males from the same cage ( $p < 0.01$ ,  $N = 35$ ). Median emergence date provides a good index for all offspring emerging from a cage, but in the case of female offspring it was confounded with the number of offspring emerging ( $r = 0.352$ ,  $p = 0.038$ ). This was not the case for male offspring ( $r = 0.014$ ,  $p = 0.94$ ). We considered the 6th to 10th emerging offspring to exclude reemerging parents, who tended to reemerge before offspring emergence began. Paternal body size had no effect on either measure of emergence time of either sex ( $r \leq 0.22$ ,  $p > 0.5$  in all cases).

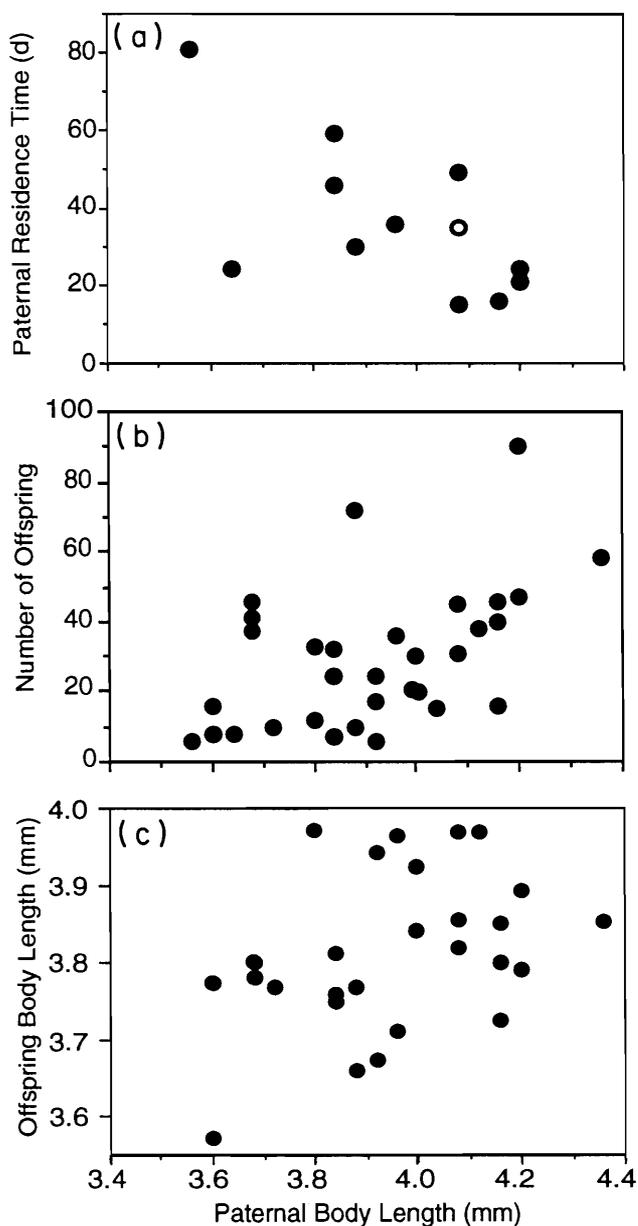
### Offspring body size

Across all offspring, body size differed slightly between females and males ( $t = 2.16$ ,  $N = 986$ ,  $p = 0.031$ ). When we examined all offspring produced for each male, we found no detectable effect of paternal body size on the mean body size of offspring (daughters:  $r = 0.16$ ,  $N = 35$ ,  $p > 0.3$ ; sons:  $r = 0.05$ ,  $N = 35$ ,  $p > 0.7$ ). However, this result is confounded because later emerging offspring tended to be smaller than early-emerging offspring (pooling all cages:  $r = -0.16$ ,  $N = 986$ ,  $p < 0.0001$ ), as has been observed for other bark beetles (Safranyik and Jahren 1970). To control for the effect of emergence date, which varied among cages, in part because of different numbers of offspring, we restricted analysis to beetles emerging during a 10-day period spanning the first pulse of emergence. This time period provided the largest sample size. We further limited analysis to those cages that produced more than one offspring during this period. The mean ( $\pm$ SD) number of beetles produced per cage during this period was thus  $7.5 \pm 1.19$  (range 2–31 beetles,  $N = 28$  cages). There was no difference in body size among female and male offspring within this more restricted data set (paired  $t$  test:  $t = 0.71$ ,  $N = 24$  cages,  $p = 0.48$ ), so we combined the sexes to give a mean body size of these offspring for each cage. We found that when emergence date was controlled, larger males produced larger offspring (Fig. 1c;  $r = 0.378$ ,  $p = 0.047$ ).

## Discussion

Larger male pine engravers deserted their broods earlier than smaller males did, as predicted by the mating opportunities hypothesis. Nevertheless, larger males also produced more offspring and generally larger offspring, as predicted by the general vigour hypothesis. The effect on offspring size was detected when emergence date was controlled by focusing on early-emerging offspring; deteriorating phloem quality experi-

**Fig. 1.** Effects of paternal body size on reproductive consequences in pine engravers, *Ips pini*. (a) Residence time for recovered marked paternal males. The open circle indicates a male that only had 1 mate (this male was excluded from the analysis). (b) Total number of offspring produced. (c) Mean offspring body size for early-emerging offspring.



enced by later emerging offspring contributes to reducing the body size of later emerging offspring (Safranyik and Jahren 1970; Anderbrant and Schlyter 1989).

The apparent paradox of both a shorter investment period and greater brood success does not necessarily pose a problem in accepting the idea that there is a trade-off between investing in individual broods and searching for additional mating opportunities. As studies of life-history theory and sexual selection have pointed out, differences in quality among individuals may result in positive correlations between two traits when compared across individuals, although the trade-off may exist within individuals (Roff 1992; Nur and

Hasson 1984). Thus, compared with a low-quality individual, a high-quality individual may invest a smaller proportion of its reproductive "budget" in a particular brood. However, because the high-quality individual has a greater budget in total, its investment in individual broods may be higher than for lower quality individuals. From the current study, it appears that larger male pine engravers can both contribute more to individual broods and have greater mating opportunities by deserting broods earlier than can smaller males.

Few previous studies have examined whether higher quality individuals spend less time with their broods, as the mating opportunities hypothesis predicts. In another bark beetle, larger males were also observed to abandon their galleries earlier (Anderbrant et al. 1985; Anderbrant 1988). In two species of birds, more attractive individuals contribute less to individual broods (Studd and Robertson 1985; Burley 1988). However, in burying beetles (*Nicrophorus* spp.) there was no detectable effect of body size on paternal residence time (Bartlett 1988; Scott and Traniello 1990), even though larger males are more successful at intrasexual competition (Scott 1990). In this case, it appears that burying beetles act as if additional breeding opportunities are very low (Scott and Gladstein 1993). Thus, the effect of parental quality on investment in individual broods may vary according to the overall likelihood of obtaining additional mating opportunities; there may even be conditions in which optimal residence time is the same for all individuals (Townsend 1986; Reid 1992).

A key question is the mechanism by which larger male pine engravers were able to produce more and larger offspring while deserting the breeding galleries earlier. One consideration is that the duration of male residence may be poorly correlated with the amount of time males actually contributed to their brood. The oviposition rate in bark beetles declines with time: most eggs are laid in the first 2 weeks of the oviposition period (M.L. Reid, unpublished data; Yearian et al. 1972; Anderbrant 1990). The earliest a male was detected to leave in this study was after 15 days. However, one male was observed to reemerge 80 days after gallery initiation, when there was little likelihood that females were still laying eggs. Thus, the large differences in residence times among males may correspond to a small difference in eggs laid.

Whether or not the duration of male residence reflects the duration of helping, we must still explain why larger males had greater reproductive success. One possibility is that larger males provided greater material benefits. Larger males may be more vigorous in cleaning the egg galleries, thereby allowing females to extend their egg galleries more quickly and to space their eggs more widely (Reid and Roitberg 1994). This would allow individual offspring to have access to more high-quality (less deteriorated) phloem, and favour greater survival and growth. Larger males may also have greater fertility or provide more nutrients to females via copulation (Fox 1993). Pine engravers copulate repeatedly during oviposition, although it appears that female *Ips* spp. can continue to lay fertile eggs in the absence of males (*I. pini*, F. Lissemore, personal communication; *I. typographus*, Anderbrant and Löfqvist 1988). In *I. typographus*, larger individuals produce more offspring than smaller individuals, given the same breeding habitat (Ander-

brant et al. 1985), but paternal and maternal effects were not distinguished in their study. These types of material benefits remained to be examined empirically in pine engravers.

The greater number and size of offspring of large males might also reflect genetic quality, as has been observed in other insects (Phelan and Baker 1986; Simmons 1987a; McLain 1991). In this case, enhanced brood success would not be dependent on male residence time, and the mating opportunities hypothesis and the general vigour hypothesis would be compatible. The effect of differences in genetic quality on reproductive success could also be enhanced by increased reproductive effort by females mated to high-quality individuals (Burley 1988). There is some evidence for such enhancement in other insects where females produce larger clutches when mated to preferred males (Hughes and Hughes 1985; Simmons 1987b). The advantage that female pine engravers could gain by investing more when mated to large males is not clear, but it could be explained if paternal size or vigour were heritable. However, there was no evidence of greater investment by females mated to larger males, whether in terms of their readiness to accept a male, in the likelihood of being recovered upon reemergence, or in the duration of female residence. Moreover, body size in bark beetles appears to be primarily environmentally determined (Anderbrant and Schlyter 1989). To distinguish experimentally whether male pine engravers contribute genetically or materially to their brood, it would be necessary to remove paternal males from galleries.

In summary, larger males deserted their broods earlier than small males did, as predicted by the mating opportunities hypothesis. Nevertheless, larger males had greater brood success, as predicted by the general vigour hypothesis. The mechanisms by which male pine engravers achieve both outcomes remain to be determined, but this study demonstrates that the superiority of larger individuals also extends to parental care. This result has important implications for male and female mating strategies and for population dynamics.

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## References

- Anderbrant, O. 1988. Survival of parent and brood adult bark beetles, *Ips typographus*, in relation to size, lipid content and re-emergence or emergence day. *Physiol. Entomol.* **13**: 121–129.
- Anderbrant, O. 1990. Gallery construction and oviposition of the bark beetle *Ips typographus* (Coleoptera: Scolytidae) at different breeding densities. *Ecol. Entomol.* **15**: 1–8.
- Anderbrant, O., and Löfqvist, J. 1988. Relation between first and second brood production in the bark beetle *Ips typographus*. *Oikos*, **53**: 357–365.
- Anderbrant, O., and Schlyter, F. 1989. Causes and effect of individual quality in bark beetles. *Holarct. Ecol.* **12**: 488–493.
- Anderbrant, O., Schlyter, F., and Birgersson, G. 1985. Intra-specific competition affecting parents and offspring in the bark beetle *Ips typographus*. *Oikos*, **45**: 89–98.
- Bartlett, J. 1988. Male mating success and paternal care in *Nicrophorus vespilloides* (Coleoptera: Silphidae). *Behav. Ecol. Sociobiol.* **23**: 297–303.
- Burley, N. 1986. Sexual selection for aesthetic traits in species with biparental care. *Am. Nat.* **127**: 415–445.
- Burley, N. 1988. The differential-allocation hypothesis: an experimental test. *Am. Nat.* **132**: 611–628.
- Carroll, S.P. 1991. The adaptive significance of mate guarding in the soapberry bug, *Jadera haematoloma* (Hemiptera: Rhopalidae). *J. Insect Behav.* **4**: 509–530.
- Cole, W.E. 1973. Crowding effects among single-age larvae of the mountain pine beetle *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *Environ. Entomol.* **2**: 285–293.
- Fox, C.W. 1993. Multiple mating, lifetime fecundity and female mortality of the bruchid beetle, *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Funct. Ecol.* **7**: 203–208.
- Gries, G. 1985. Zur Frage der Dispersion des Buchdruckers (*Ips typographus* L.). [As to the question of dispersal in (*Ips typographus* L.).] *Z. Angew. Entomol.* **99**: 12–20.
- Hughes, A.L., and Hughes, M.K. 1985. Female choice of mates in a polygynous insect, the white-spotted sawyer *Monochamus scutellatus*. *Behav. Ecol. Sociobiol.* **17**: 385–387.
- Keenleyside, M.A. 1983. Mate desertion in relation to adult sex ratio in the biparental cichlid fish *Herotilapia multispinosa*. *Anim. Behav.* **31**: 683–688.
- Langor, D.W., and Raske, A.G. 1987. Emergence, host attack, and overwintering behavior of the eastern larch beetle, *Dendroctonus simplex* LeConte (Coleoptera: Scolytidae), in Newfoundland. *Can. Entomol.* **119**: 975–983.
- Maynard Smith, J. 1977. Parental investment: a prospective analysis. *Anim. Behav.* **25**: 1–9.
- McLain, D.K. 1989. Prolonged copulation as a post-insemination guarding tactic in a natural population of the ragwort seed bug. *Anim. Behav.* **38**: 659–664.
- McLain, D.K. 1991. Heritability of size: a positive correlate of multiple fitness components in the southern green stink bug (Hemiptera: Pentatomidae). *Ann. Entomol. Soc. Am.* **84**: 174–178.
- Nur, N., and Hasson, O. 1984. Phenotypic plasticity and the handicap principle. *J. Theor. Biol.* **110**: 275–297.
- Phelan, P.L., and Baker, T.C. 1986. Male-size-related courtship success and intersexual selection in the tobacco moth, *Ephestias elutella*. *Experientia*, **42**: 1291–1293.
- Reid, M.L. 1992. Female mate choice and male parental care in a bark beetle (*Ips pini*, Coleoptera: Scolytidae). Ph.D. thesis, Simon Fraser University, Burnaby, B.C.
- Reid, M.L., and Roitberg, B.D. 1994. Benefits of prolonged residence with mates and brood in a bark beetle (Coleoptera: Scolytidae). *Oikos*, **70**: 140–148.
- Reiss, M.J. 1989. The allometry of growth and reproduction. Cambridge University Press, Cambridge.
- Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. *Oikos*, **44**: 257–267.
- Roff, D.A. 1992. The evolution of life histories. Chapman and Hall, Inc., New York.
- Safranyik, L. 1976. Size- and sex-related emergence, and survival in cold storage, of mountain pine beetles. *Can. Entomol.* **108**: 209–212.
- Safranyik, L., and Jähren, R. 1970. Emergence patterns of the mountain pine beetle from lodgepole pine. *Can. Dep. Fish. For. Bi-Mon. Res. Notes*, **26**: 11–12.
- Schenk, J.A., and Benjamin, D.M. 1969. Notes on the biology of

- Ips pini* in central Wisconsin jack pine forests. *Ann. Entomol. Soc. Am.* **62**: 480–485.
- Scott, M.P. 1990. Brood guarding and the evolution of male parental care in burying beetles. *Behav. Ecol. Sociobiol.* **26**: 31–39.
- Scott, M.P., and Gladstein, D.S. 1993. Calculating males? An empirical and theoretical examination of the duration of paternal care in burying beetles. *Evol. Ecol.* **7**: 362–378.
- Scott, M.P., and Traniello, J.F.A. 1990. Behavioural and ecological correlates of male and female parental care and reproductive success in burying beetles (*Nicrophorus* spp.). *Anim. Behav.* **39**: 274–283.
- Simmons, L.W. 1987a. Heritability of a male character chosen by females of the field cricket *Gryllus bimaculatus*. *Behav. Ecol. Sociobiol.* **21**: 129–133.
- Simmons, L.W. 1987b. Female choice contributes to offspring fitness in the field cricket, *Gryllus bimaculatus* (De Geer). *Behav. Ecol. Sociobiol.* **21**: 313–321.
- Studd, M.V., and Robertson, R.J. 1985. Sexual selection and variation in reproductive strategy in male yellow warblers (*Dendroica petechia*). *Behav. Ecol. Sociobiol.* **17**: 101–109.
- Swaby, J.A., and Rudinsky, J.A. 1976. Acoustic and olfactory behaviour of *Ips pini* (Say) (Coleoptera: Scolytidae) during host invasion and colonisation. *Z. Angew. Entomol.* **81**: 421–432.
- Thompson, S.N., and Bennett, R.B. 1971. Oxidation of fat during flight of male Douglas-fir beetles, *Dendroctonus pseudotsugae*. *J. Insect Physiol.* **17**: 1555–1563.
- Thornhill, R., and Alcock, J. 1983. The evolution of insect mating systems. Harvard University Press, Cambridge, Mass.
- Townsend, D.S. 1986. The costs of male parental care and its evolution in a neotropical frog. *Behav. Ecol. Sociobiol.* **19**: 187–195.
- Trivers, R.L. 1972. Parental investment and sexual selection. In *Sexual selection and the descent of man, 1871–1971*. Edited by B. Campbell. Aldine, Chicago. pp. 136–179.
- Winkler, D.W. 1987. A general model for parental care. *Am. Nat.* **130**: 526–543.
- Yearian, W.C., Gouger, R.J., and Wilkinson, R.C. 1972. Effects of the bluestain fungus, *Ceratocystis ips*, on development of *Ips* bark beetles in pine bolts. *Ann. Entomol. Soc. Am.* **65**: 481–487.