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Reproductive allocation and reproductive ecology of seven species of Diptera

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Abstract. 1. Variation in resource allocation to egg size and number was investigated in seven sympatric species of Piophilidae that oviposit on carcasses or discarded cervid antlers: *Liopiophila varipes* (Meigen), *Prochyliza xanthostoma* Walker, *Protopiophila latipes* (Meigen), *Protopiophila litigata* Bonduriansky, *Stearibia nigriceps* (Meigen), and two unidentified species of *Parapiophila* McAlpine.

2. Following optimal reproductive allocation theory, relatively larger, fewer eggs were expected in (1) species that oviposit on antlers, where larvae probably experience lower risk of predation and greater competition than larvae in carcasses, and (2) species with aggressive males and male-biased sex ratios on the oviposition substrate, where risk of injury during oviposition may have favoured females laying fewer eggs.

3. Variation in reproductive allocation strategies could not be explained by known differences in larval or adult environment, but congeneric species clustered by reproductive allocation patterns. The *Parapiophila* species produced larger, fewer eggs than the other species, and egg number increased slowly with body size. The *Protopiophila* species did not deviate from expected egg sizes and numbers, and egg number increased steeply with body size.

4. An interspecific egg size–egg number trade-off resulted in a tight linear scaling of ovary volume to body size, suggesting common physiological constraints on relative ovary mass.

5. Within each species, egg size was nearly constant whereas egg number increased with female body size, suggesting species-specific stabilising selection on egg size.

Key words. Diptera, egg size, Piophilidae, reproductive allocation, trade-off.

Introduction

Reproductive allocation strategies evolve in response to environmental or demographic conditions (Stearns, 1976; Parker & Begon, 1986) but they may also be subject to nonadaptive allometric constraints, or *phylogenetic inertia*, the tendency to retain the ancestral condition (Wiklund *et al*., 1987; Marshall & Gittleman, 1994). Several studies have investigated variation in reproductive allocation within or among arthropod species (e.g. Stewart *et al*., 1991; Hard & Bradshaw, 1993), and some of these attempted to relate interspecific variation in egg size and number to variation in ecological factors, such as ovipositional substrates (e.g. Kambysellis & Heed, 1971; Montague *et al*., 1981). Such data are still distributed sparsely among taxonomic groups, and broader patterns are just beginning to emerge.

The pattern of reproductive allocation, or relation between size and number of offspring, is an important component of maternal fitness (Smith & Fretwell, 1974). If the total quantity of resources available for reproduction is finite, offspring size and number cannot vary independently: a trade-off must occur. Moreover, if the fitness of an individual offspring is related to the quantity of resources invested in it (e.g. size of the egg), females will be selected to optimise egg size and number so as to maximise their fitness (Parker & Begon, 1986). A trade-off between egg size and number has been reported in several studies (e.g. Cook *et al*., 1989; Berrigan, 1991a; but see Marshall & Gittleman, 1994).

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According to the model of Parker and Begon (1986), egg size may be subject to species-specific stabilising selection, so that egg number will increase with female body size within each species while egg size will not. Intense larval competition for resources may favour larger investment per offspring, however, so that larger females produce larger eggs. Among species, production of large eggs may be favoured by intense larval competition (Parker & Begon, 1986; McLain & Mallard, 1991) and, perhaps, by low risk of predation (Wilbur *et al*., 1974; McLain & Mallard, 1991). Risk incurred by females during oviposition may also select for a reduction in the number of eggs, in order to reduce oviposition time (Wilson & Lessells, 1994).

These predictions of optimal reproductive allocation theory were tested using seven sympatric species of the subtribe Piophilina (Piophilidae) that oviposit on carcasses or discarded cervid antlers (Fig. 1). Although a discarded antler contains much less edible matter per unit mass than a carcass, a moose antler can serve as a larval medium for up to 5 years (Bonduriansky, 1996), whereas a carcass rarely lasts more than a few weeks (Bornemissza, 1957; Payne, 1965). Thus, larval fitness is probably limited more by access to food in antlers than in carcasses, resulting in more intense larval competition inside antlers. Furthermore, carcasses attract a variety of beetles that prey on dipteran larvae (Chapman & Sankey, 1955; Reed, 1958), whereas maggots inhabiting the narrow bone-canals inside antlers are inaccessible to predators (Bonduriansky, 1996). For both reasons, antler specialists were expected to produce larger (and fewer) eggs than carcass specialists. In addition, males of some piophilid species are extremely aggressive, frequently harass females, and outnumber females on the oviposition substrate (Bonduriansky, 1996). *Protopiophila litigata* females sometimes limp away with broken wings or legs from pairs of grappling suitors (Bonduriansky & Brooks, 1998). Hence, females of such species were expected to produce fewer (and larger) eggs than those of other species. Alternatively, interspecific variation in reproductive allocation may simply correspond to phylogenetic relationships, indicated by clustering of congeneric species.

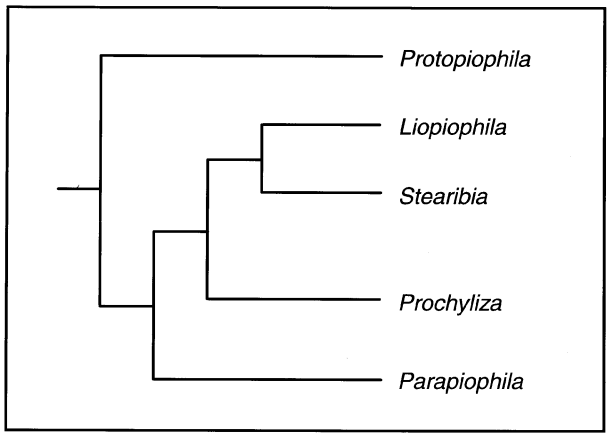

Fig. 1. A phylogeny of the subtribe Piophilina (Piophilidae). Modified from McAlpine (1977) (some genera not shown).

Materials and methods

Reproductive allocation parameters

Females of *Liopiophila varipes* (Meigen) ($n = 10$), *Prochyliza xanthostoma* Walker ($n = 10$), *Protopiophila latipes* (Meigen) ($n = 16$), *Protopiophila litigata* Bonduriansky ($n = 211$), *Stearibia nigriceps* (Meigen) ($n = 10$), and two unidentified species of *Parapiophila* McAlpine, labelled 'sp. 1' ($n = 10$) and 'sp. 2' ($n = 20$), were collected from carcasses (fish, rodents, moose) and discarded moose (*Alces alces* L.) antlers at the Wildlife Research Station, Algonquin Provincial Park, Ontario, Canada (45°30′N, 78°40′W) from June to August 1995. Females were killed by freezing, thawed, and glued dorsally to paper labels. For each female, body length, from posterior tip of abdomen to anterior tip of antennal flagellum, and head width were estimated to 0.01 mm using a dissecting microscope with an ocular micrometer. The abdomen was then severed with a microscalpel and placed in a drop of isotonic solution (pond water), and the ovaries were removed using microprobes. The number of ovarioles was determined, and the lengths of 10 (where possible) randomly selected mature eggs were measured. Because eggs did not vary appreciably in width among or within conspecific females, a single estimate of egg width was obtained for each species.

Female body size was estimated as the volume of a cylinder (body size = 1/4 × body length × π × head width^2), and egg size was estimated as the volume of an ellipsoid (egg size = 1/6 × egg length × π × egg width^2). Rates of egg maturation and deposition are not known in these flies but, because females of these species produce only one mature egg at a time per ovariole (R. Bonduriansky, pers. obs.), the number of ovarioles (*egg number*) is likely to be correlated strongly with the number of eggs produced and laid over the female's lifetime, and egg size × egg number (*ovary volume*) represents the total volume of mature eggs carried by a fully gravid female. An egg size–egg number trade-off can be detected as a negative correlation between residual values from two regressions: (1) body size and egg size, and (2) body size and egg number (Berrigan, 1991a). Statistical tests were performed using Statistica (Release 5.01995; StatSoft, Inc., Tulsa, Oklahoma).

Ecology and behaviour

Behaviours of each species were observed and specimens were collected in the field on carcasses (fish, rodents, moose) or discarded moose antlers from May to August 1994–95, at the Wildlife Research Station. Some specimens were trapped in a plastic box (≈ 40 × 25 × 10 cm) with a heavy, tightly shutting lid hinged at one end. A piece of carcass in an envelope of fine copper mesh was placed inside the box, and the lid was propped open with a stick. Flies were captured by

pulling a string attached to the stick, causing the lid to slam shut, and killed by placing the box in a freezer. Collections obtained using this technique are free of sex or taxon bias. Other specimens were collected by covering them with small jars. Specimens obtained by different methods were pooled because interspecific differences were quite consistent across all collections. Flies were identified and sexed using keys in McAlpine (1977) and Bondurianskiy (1995), and deposited in the University of Guelph Insect Collection.

Results

Ecology, behaviour, and sex ratio

Protopiophila spp. adults were active from early June to late August; adults of the other species were active from late May to late August. *Protopiophila litigata* specialised on discarded antlers as its ovipositional substrate, *Parapiophila* sp. 2 used both antlers and carcasses, and all other species used carcasses only (Table 1). *Stearibia nigriceps*, *P. xanthostoma*, and both *Parapiophila* species favoured carcasses in intermediate stages of decay, whereas *P. latipes* and *L. varipes* favoured carcasses at later stages of decay. Sex ratio on ovipositional substrates was male-biased in *P. litigata*, *P. latipes*, and *L. varipes*, female-biased in both *Parapiophila* species, and unbiased in *S. nigriceps* and *P. xanthostoma* (Table 1). *Protopiophila litigata*, *P. latipes*, and *L. varipes* males were also very aggressive and often harassed (i.e. chased or wrestled over) ovipositing females. *Prochyliza xanthostoma* males boxed other males with their forelegs and performed side-to-side displays in front of males and females, but did not appear to harass females. *Stearibia nigriceps* and *Parapiophila* spp. males did not fight other males or visibly harass females.

Reproductive allocation patterns

Among *P. litigata*, *P. latipes*, *S. nigriceps*, *L. varipes*, and *P. xanthostoma*, mean egg size increased with mean body size ($n = 113$ gravid females, $r = 0.75$, $F = 145.7$, $P < 0.001$), as did the mean number of ovarioles ($n = 221$ females, $r = 0.82$, $F = 453.3$, $P < 0.001$) (Table 2, Fig. 2). For all seven species, residual values from regression of mean body size and mean egg size were correlated negatively with residual values from regression of mean body size and mean number of ovarioles ($n = 7$ species, $r = -0.97$, $F = 74.71$, $P < 0.001$), indicating an interspecific egg size–egg number trade-off. Among all gravid females, ovary volume was an increasing function of body size ($n = 114$, $r = 0.94$, $F = 805.96$, $P < 0.001$) (Fig. 3). The two

Table 1. Number of males and females of seven species of Piophilidae collected from carcasses and discarded moose antlers (May to August 1994–95), and χ^2-tests (d.f. = 1) for sex-ratio bias.

Species	From carcasses	χ^2	*P*	From antlers	χ^2	*P*
P. litigata	2♂,8♀	3.6	NS	1396♂,583♀	334	<0.001
P. latipes	67♂,31♀	13.22	<0.001	1♀	–	–
S. nigriceps	53♂,70♀	2.35	NS	0	–	–
L. varipes	102♂,20♀	55.11	<0.001	1♂	–	–
P. xanthostoma	23♂,18♀	0.61	NS	1♂	–	–
Parapiophila sp.1	6♂,21♀	8.33	<0.005	3♀	–	–
Parapiophila sp.2	8♂,77♀	56.01	<0.001	5♂,117♀	102.8	<0.001

Table 2. Means and standard deviations (SD) for body size of all females, number of ovarioles, body size of gravid females, and egg size for seven species of Piophilidae.

Species	Total females	Mean female body size, $mm^3 \pm SD$	Mean number of ovarioles ± SD	Gravid females (per cent of total)	Mean body size, gravid females ± SD	Egg size, $mm^3 \times 10^5 \pm SD$
P. litigata	211*	1.16 ± 0.251	31.89 ± 8.55	93 (44)†	1.17 ± 0.269	345 ± 21.1
P. latipes	16	1.61 ± 0.418	46.56 ± 16.02	3 (19)	1.95 ± 0.721	585 ± 20.7
S. nigriceps	10	2.27 ± 0.858	50.00 ± 24.76	7 (70)	2.53 ± 0.903	674 ± 23.9
L. varipes	10	2.23 ± 0.881	41.10 ± 13.84	4 (40)	2.02 ± 0.664	667 ± 24.6
P. xanthostoma	10	2.73 ± 0.920	61.80 ± 19.50	6 (60)	2.84 ± 0.987	715 ± 37.9
Parapiophila sp. 1	10	2.39 ± 0.632	41.30 ± 10.54	9 (90)	2.45 ± 0.645	936 ± 35.2
Parapiophila sp. 2	20‡	2.33 ± 0.661	22.80 ± 4.95	11 (55)	2.71 ± 0.465	1677 ± 59.8

*Number of ovarioles known for $n = 176$ females.
†Number of ovarioles known for $n = 74$ gravid females.
‡Number of ovarioles known for $n = 15$ females.

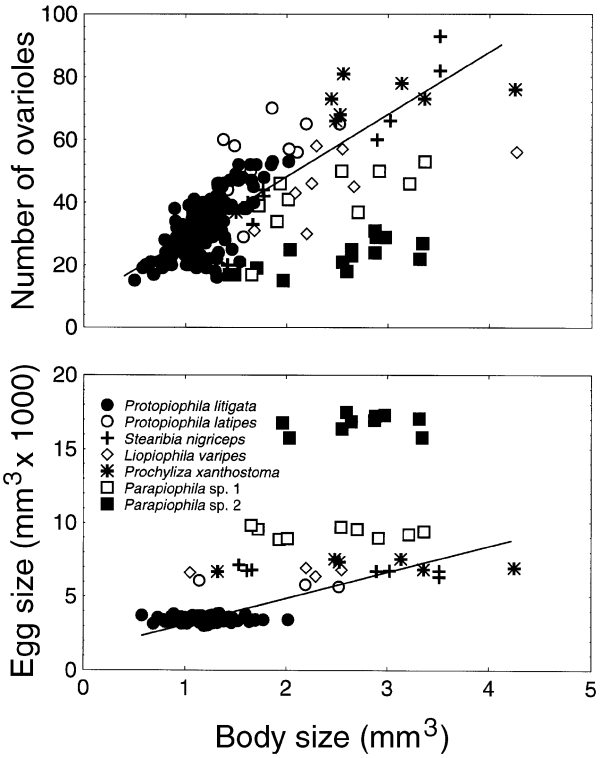

Fig. 2. Egg size and body size and number of ovarioles and body size for seven species of Piophilidae (see Table 3); *Parapiophila* sp. 1 and sp. 2 were not included in the regression.

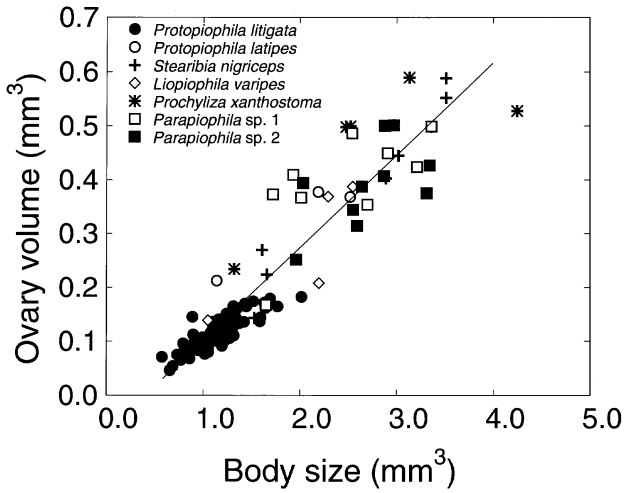

Fig. 3. Regression of ovary volume and body size for seven species of Piophilidae.

Parapiophila species had larger eggs and fewer ovarioles than expected for their body sizes, and exhibited a distinct pattern of egg size–ovariole number covariation ($n = 19$, $r = -0.79$, $F = 27.77$, $P < 0.001$) relative to the other species ($n = 94$, $r = 0.59$, $F = 48.53$, $P < 0.001$) (Fig. 4).

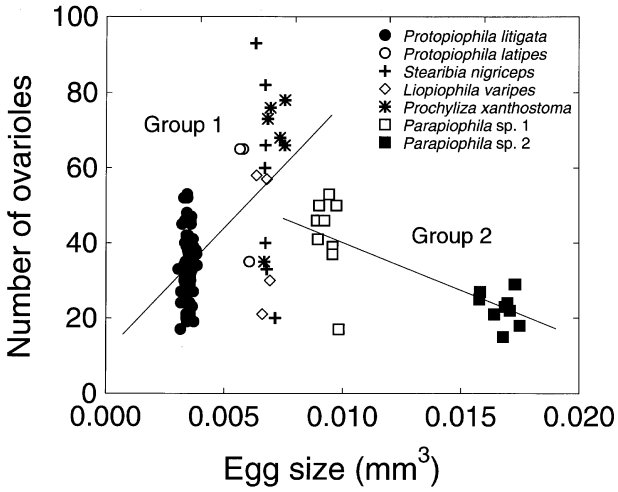

Fig. 4. Regressions of number of ovarioles and egg size for two groups of piophilid species. Group 1: *P. litigata*, *P. latipes*, *S. nigriceps*, *L. varipes*, and *P. xanthostoma*; Group 2: *Parapiophila* sp. 1, *Parapiophila* sp. 2.

As expected, egg size did not covary with body size within any species, whereas number of ovarioles increased with body size within each species (Table 3, Fig. 2). This pattern represents a robust result for the subtribe Piophilina despite some small sample sizes because relationships of body size with egg size and number were qualitatively similar in all species, and consistent with a prediction of optimal reproductive allocation theory. Slopes from intraspecific regressions of body size and number of ovarioles (Table 3) were not all equal (one-factor ANOVA: d.f. = 6,238, $F = 10.39$, $P < 0.001$). Multiple contrasts (Scheffé's tests) were performed to determine whether species clustered by ovipositional substrate or by phylogeny (i.e. genus). The *Protopiophila* species and *S. nigriceps* had higher slopes than *L. varipes* and the *Parapiophila* species ($S = 7.24$, $P < 0.05$), and higher slopes than *P. xanthostoma* ($S = 3.76$, $P < 0.05$), whereas *P. xanthostoma* did not have a higher slope than *L. varipes* and the *Parapiophila* species ($S = 1.46$, $P > 0.05$). Hence, congeneric species clustered by the slope of the body size-ovariole number regression.

Discussion

Variation in reproductive allocation strategies

Among the seven piophilid species, two basic reproductive allocation strategies could be distinguished: (1) a small number of large eggs (*Parapiophila* spp.) and (2) egg size and number both close to expected values (the other five species) (Table 4). Is it possible to account for these strategies as adaptations to larval or adult environments?

According to optimal reproductive allocation theory, large eggs are favoured by intense competition for resources at the

Table 3. Intraspecific regressions of body size (mm^3) and number of ovarioles, and body size and egg size (mm^3) for seven species of Piophilidae; slopes followed by different letters are significantly different (Scheffé's test).

	Body size–ovariole number				Body size–egg size		
Species	*n*	*r*	Slope	*F*	*n*	*r*	*F*
P. litigata	176	0.75	25.29[a]	222.2 ***	92	0.09	0.8 (NS)
P. latipes	16	0.72	27.63[a]	15.1 **	3	0.99	70.4 (NS)
S. nigriceps	10	0.96	27.65[a]	89.7 ***	7	−0.68	4.3 (NS)
L. varipes	10	0.76	11.91[b]	10.8 *	4	0.18	0.1 (NS)
P. xanthostoma	9	0.79	15.14[b]	11.8 *	6	0.09	0.0 (NS)
Parapiophila sp. 1	10	0.68	11.34[b]	6.9 *	9	0.14	0.1 (NS)
Parapiophila sp. 2	15	0.69	5.53[b]	12.1 **	10	0.19	0.3 (NS)

NS = not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 4. Larval habitat, months of adult activity, sex ratio bias, male harassment of females, relative slope of the intraspecific body size–egg number regression, and reproductive allocation strategy for each of seven species of Piophilidae.

Species	Larval habitat	Months of adult activity	Sex ratio bias	Body size–egg number slope	Males harass females	Reproductive allocation strategy
P. litigata	Antlers	June–August	Male	High	Yes	Egg size and number as expected
P. latipes	Carcasses	June–August	Male	High	Yes	Egg size and number as expected
S. nigriceps	Carcasses	May–August	None	High	No	Egg size and number as expected
L. varipes	Carcasses	May–August	Male	Low	Yes	Egg size and number as expected
P. xanthostoma	Carcasses	May–August	None	Low	?	Egg size and number as expected
Parapiophila sp. 1	Carcasses	May–August	Female	Low	No	Egg size large, number small
Parapiophila sp. 2	Carcasses, Antlers	May–August	Female	Low	No	Egg size large, number small

larval stage (Parker & Begon, 1986; McLain & Mallard, 1991), and possibly by low risk of predation on larvae (Wilbur *et al*., 1974; McLain & Mallard, 1991). Because discarded antlers offer a poor but long-lasting resource in comparison with carcasses, and larvae inside antlers are comparatively safe from predation by carrion beetles (Reed, 1958; Payne, 1965; Bonduriansky, 1996), species that oviposit on antlers were expected to produce larger (and fewer) eggs than species that oviposit on carcasses. Instead, the two species that oviposited on antlers utilised very different reproductive allocation strategies: *P. litigata*, an antler specialist, did not deviate from the egg size expected for its body size, whereas *Parapiophila* sp. 2, which used both antlers and carcasses, produced larger eggs than expected. Similarly, among the carcass specialists, *Parapiophila* sp. 1 produced much larger eggs than the other species. Thus, variation in reproductive allocation strategies cannot be attributed to obvious differences between ovipositional substrates. This does not preclude the possibility that the variation is related to factors not considered in this study, such as microenvironmental aspects of larval niches (Kambysellis & Heed, 1971), or the particular way in which larval density affects larval fitness (Ives, 1989).

Species where females risk being injured by males were expected to produce fewer, larger eggs. Because selection was expected to reduce total oviposition time (Wilson & Lessells, 1994), the number of ovarioles (which is related to the total number of eggs a female will produce) is a more appropriate variable for analysis than the way in which these eggs are distributed among oviposition bouts (i.e. mean *clutch size*). The results did not support the predictions. Species where males outnumber and physically harass females (*P. litigata*, *P. latipes*, *L. varipes*) did not deviate from the egg sizes and numbers expected for their body sizes, whereas two species with unaggressive males and female-biased sex ratios (*Parapiophila* spp.) produced fewer, larger eggs than expected. These results suggest that male harassment does not select for a reduction in the number of eggs females lay. This study may have been the first to test this hypothesis.

Reproductive allocation and phylogeny

Congeneric species utilised similar reproductive allocation strategies, even though they used different ovipositional substrates (Table 4). Both *Protopiophila* species produced egg sizes and numbers close to expected values for their body sizes, even though they used different oviposition substrates. Both *Parapiophila* species produced relatively few, large eggs, even though sp. 1 was a carcass specialist and sp. 2 used both carcasses and antlers. Although adaptive causes have not been

ruled out, these results suggest that reproductive allocation patterns are constrained by *phylogenetic inertia* in the subtribe Piophilina, at least at the level of congeneric species. Clustering of related species by reproductive allocation parameters also occurs among some water mites (Arrenuridae) (Cook *et al*., 1989).

Interspecific egg size–egg number trade-off and reproductive effort

Among species (excluding *Parapiophila* spp.), mean egg size and mean egg number increased with female body size. An egg size–egg number trade-off was detected among all seven species, indicated by strong negative correlation between residual values for mean egg size and residual values for mean egg number. Similarly, Berrigan (1991a) reported positive correlations of mean body size with mean egg size and mean egg number among drosophilid species, and detected egg size–egg number trade-offs among species of Diptera, Hymenoptera, and Coleoptera. In contrast, Marshall and Gittleman (1994) observed no such trade-off among species of spiders (Araneomorphae). It is not clear why interspecific trade-offs are detected in some taxa but not in others.

The interspecific egg size–egg number trade-off resulted in a tight linear scaling of ovary volume to body size. Assuming that egg composition is similar in these seven species, so that ovary volume is a good predictor of ovary mass, this suggests that the ovary mass : body mass ratio (*relative ovary mass*) is constrained to a particular trajectory of interspecific variation, or 'some common law of growth' (Wiklund *et al*., 1987). The number of ovarioles (*egg number*) was used to calculate ovary mass because stabilising selection on relative ovary mass in these species is most likely to limit the number of ovarioles (i.e. number of eggs carried by a fully gravid female) rather than the mean *clutch size* deposited per oviposition bout. Even if egg compositions and egg maturation rates vary somewhat among these closely related species, relative ovary mass is probably correlated strongly with reproductive effort. Because reproductive effort is closely related to fitness (Williams, 1966), it can be limited only by factors that reduce survivorship (Shine & Schwarzkopf, 1992). The ability to generate lift during take-off may be such a factor because it is related to the ability to escape from predators (Berrigan, 1991b). If the increased abdomen mass associated with egg development reduces females' ability to generate lift, fecundity gains from increased relative ovary mass will be balanced by increased risk of mortality. Because lift production is proportional to muscle mass (Marden, 1987; Berrigan, 1991b), the interspecific scaling of ovary mass to body mass may be determined by the scaling of muscle mass to body mass in the subtribe Piophilina.

Variation within species

Within each species, egg size was nearly constant, while egg number increased with female body size. This suggests that the *intrinsic effects* of egg size result in strong stabilising selection (Parker & Begon, 1986), causing larger females to invest their extra resources in increased egg number (i.e. increased number of ovarioles). Low intraspecific variation in egg size has been reported for several other insect species, such as the tephritid flies *Dacus tryoni* (Frogg.) and *D. jarvisi* (Tryon) (Fitt, 1990). Directional selection on egg size was reported in the bug *Nezara viridula* L. (McLain & Mallard, 1991). Egg size is probably subject to a combination of stabilising selection (e.g. from physiological constraints on offspring size and/or limits on duration of larval development) and directional selection (e.g. from higher competitive ability of larger individuals) in most insects. The exact nature of those selective forces, and even their net effects on egg size, remain to be discovered in most insect groups.

Conclusions

Variation in egg size and number among seven sympatric piophilid species was not consistent with predictions from optimal reproductive allocation models (e.g. Parker & Begon, 1986; Wilson & Lessells, 1994), based on apparent differences in larval and adult environments experienced by these species. Instead, variation in reproductive allocation patterns corresponded to phylogenetic relationships. Patterns of intraspecific variation suggest that egg size is subject to species-specific stabilising selection in the subtribe Piophilina. These results highlight the need to test and refine the predictions of optimal reproductive allocation models.

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References

Berrigan, D. (1991a) The allometry of egg size and number in insects. *Oikos*, **60**, 313–321.

Berrigan, D. (1991b) Lift production in the flesh fly, *Neobellieria* (= *Sarcophaga*) *bullata* Parker. *Functional Ecology*, **5**, 448–456.

Bonduriansky, R. (1995) A new Nearctic species of *Protopiophila* Duda (Diptera: Piophilidae), with notes on its behaviour and comparison with *P. latipes* (Meigen). *Canadian Entomologist*, **127**, 859–863.

Bonduriansky, R. (1996) *Effects of body size on mate choice and fecundity in the antler fly,* Protopiophila litigata *(Diptera: Piophilidae).* MSc thesis, University of Guelph, Canada.

Bonduriansky, R. & Brooks, R.J. (1998) Copulation and oviposition behaviour of *Protopiophila litigata* (Diptera: Piophilidae). *Canadian Entomologist*, **130**, 399–405.

Bornemissza, G.F. (1957) An analysis of arthropod succession in carrion and the effect of its decomposition on the soil fauna. *Australian Journal of Zoology*, **5**, 1–12.

Chapman, R.F. & Sankey, J.H.P. (1955) The larger invertebrate fauna of three rabbit carcasses. *Journal of Animal Ecology*, **24**, 395–402.

Cook, W.J., Smith, B.P. & Brooks, R.J. (1989) Allocation of reproductive effort in female *Arrenurus* spp. water mites (Acari: Hydrachnidia; Arrenuridae). *Oecologia*, **79**, 184–188.

Fitt, G.P. (1990) Comparative fecundity, clutch size, ovariole number and egg size of *Dacus tryoni* and *D. jarvisi*, and their relationship to body size. *Entomologia experimentalis et applicata*, **55**, 11–21.

Hard, J.J. & Bradshaw, W.E. (1993) Reproductive allocation in the western tree-hole mosquito, *Aedes sierrensis*. *Oikos*, **66**, 55–65.

Ives, A.R. (1989) The optimal clutch size of insects when many females oviposit per patch. *American Naturalist*, **133**, 671–687.

Kambysellis, M.P. & Heed, W.B. (1971) Studies of oogenesis in natural populations of Drosophilidae. I. Relation of ovarian development and ecological habitats of the Hawaiian species. *American Naturalist*, **105**, 31–49.

Marden, J.H. (1987) Maximum lift production during takeoff in flying animals. *Journal of Experimental Biology*, **130**, 235–258.

Marshall, S.D. & Gittleman, J.L. (1994) Clutch size in spiders: is more better? *Functional Ecology*, **8**, 118–124.

McAlpine, J.F. (1977) A revised classification of the Piophilidae, including 'Neottiophilidae' and 'Thyreophoridae' (Diptera: Schizophora). *Memoirs of the Entomological Society of Canada*, **103**, 1–66.

McLain, D.K. & Mallard, S.D. (1991) Sources and adaptive consequences of egg size variation in *Nezara viridula* (Hemiptera: Pentatomidae). *Psyche*, **98**, 135–164.

Montague, J.R., Mangan, R.L. & Starmer, W.T. (1981) Reproductive allocation in the Hawaiian Drosophilidae: egg size and number. *American Naturalist*, **118**, 865–871.

Parker, G.A. & Begon, M. (1986) Optimal egg size and clutch size: effects of environment and maternal phenotype. *American Naturalist*, **128**, 573–592.

Payne, J.A. (1965) A summer carrion study of the baby pig *Sus scrofa* Linnaeus. *Ecology*, **46**, 592–602.

Reed, H.B., Jr (1958) A study of dog carcass communities in Tennessee, with special reference to the insects. *American Midland Naturalist*, **59**, 213–245.

Shine, R. & Schwarzkopf, L. (1992) The evolution of reproductive effort in lizards and snakes. *Evolution*, **46**, 62–75.

Smith, C.C. & Fretwell, S.D. (1974) The optimal balance between size and number of offspring. *American Naturalist*, **108**, 499–506.

Stearns, S.C. (1976) Life-history tactics: a review of the ideas. *Quarterly Review of Biology*, **51**, 3–47.

Stewart, L.A., Dixon, A.F.G., Ruzicka, Z. & Iperti, G. (1991) Clutch and egg size in ladybird beetles. *Entomophaga*, **36**, 329–333.

Wiklund, C., Karlsson, B. & Forsberg, J. (1987) Adaptive versus constraint explanations for egg-to-body size relationships in two butterfly families. *American Naturalist*, **130**, 828–838.

Wilbur, H.M., Tinkle, D.W. & Collins, J.P. (1974) Environmental certainty, trophic level, and resource availability in life history evolution. *American Naturalist*, **108**, 805–817.

Williams, G.C. (1966) Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist*, **100**, 687–690.

Wilson, K. & Lessells, C.M. (1994) Evolution of clutch size in insects. I. A review of static optimality models. *Journal of Evolutionary Biology*, **7**, 339–363.

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