

Short communications

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Reproduction, development and diet of *Parasitellus fucorum* (Mesostigmata: Parasitidae), a mite associated with bumblebees (Hymenoptera: Apidae)

S. Koulianos and H. H. Schwarz

Experimentelle Oekologie, ETH Zürich, ETH Zentrum NW, CH-8092 Zürich, Switzerland

Abstract

The mite *Parasitellus fucorum* (De Geer) (Mesostigmata: Parasitidae) lives and reproduces in the nests of bumblebees. Despite its abundance on European bumblebees and its occasional invasion of honeybee nests, little is known about its basic life-history traits and dietary requirements. This paper describes the mating behaviour, oviposition and development of *P. fucorum* under controlled laboratory conditions, and provides observations on the dietary preferences of its life-cycle stages.

Key words: acari, development, diet, mating, oviposition, *Parasitellus fucorum*

INTRODUCTION

Of the wide variety of arthropods that colonize the nests of social insects, mites are the most diverse and numerous (Eickwort, 1990). Many mite species have specialized on one insect lineage, and some can be either beneficial or harmful to their host (Eickwort, 1994; Schmid-Hempel, in press). Although there is an increasing literature on the few mites that are pathogenic to domesticated honeybees, there is little information on the biology and behaviour of other mite species associated with social insects.

The mite *Parasitellus fucorum* (De Geer) (Mesostigmata: Parasitidae) lives and reproduces in the nests of bumblebees (Vitzthum, 1930). The life-cycle of *P. fucorum* is typical for mesostigmatic mites and comprises five stages: egg, larva, protonymph, deutonymph and adult. The deutonymphs disperse by attaching to adult bumblebees for transport (Huck, Schwarz & Schmid-Hempel, 1998). In autumn, when the bumblebee colony declines and workers, males and the old queen die, the deutonymphs attach to the young queens, which overwinter singly in the soil. When an overwintered queen founds a new colony in spring, the deutonymphs detach and moult into adults that colonize the new nest. Despite the abundance of *P. fucorum* on European bumblebees (Schousboe, 1987; Schwarz, Huck, & Schmid-Hempel, 1996) and its occasional invasion of honeybee hives (De Jong, Morse, & Eickwort, 1982), little is known about its basic life-history traits and dietary requirements.

In this paper we report on the mating behaviour,

oviposition, and development of *P. fucorum* under controlled laboratory conditions, and provide observations on the dietary preferences of its life-cycle stages.

MATERIALS AND METHODS

Foraging queens of *Bombus terrestris* (L.) were caught in Weiningen, Switzerland in May 1994 for use in the mating experiments. In the laboratory, the bees were anaesthetized in a stream of CO₂ and the adhering deutonymphs removed. Deutonymphs of *P. fucorum* were identified by size and the triangular shape of their opisthonotal shield (Hyatt, 1980), and put groups of 5–8 into clear plastic boxes (50 × 30 × 16 mm) half filled with moist peat. As the kind of food the deutonymphs require to induce adult moult was not known, each box was supplied with: a piece of dead mealworm, a small dish of sugar-water, and a pollen ball freshly removed from the corbiculum of a field-caught bumblebee (commercially available pollen collected by honeybees was not accepted by the mites; pers. obs.). The plastic boxes were kept in the dark at 21 ± 1 °C and checked daily. At each check the peat was moistened, old food exchanged with fresh, and newly moulted adults removed for the mating experiments. Adult females were only used for mating experiments if there were no adult males in the same box, to ensure that they were unmated.

In the mating experiments, pairs of newly moulted (<24 h old) males and females were put into plastic arenas (50 × 30 × 16 mm) lined with moist filter paper. Each pair was observed continuously with a stereo

Table 1. Life-history traits of *P. fucorum* ($n = 11$ pairs)

Trait	Mean	SD	Range
Mating duration (min)	67.8	93.4	5–322
No. of eggs laid	102.1	59.7	33–214
Oviposition period (days)	7.1	2.9	3–13
Female longevity (days)	27.6	10.0	20–55
Duration of offspring development (days) ^a			
Egg	2.8	0.4	2.0–3.2
Larva	2.2	0.4	2.0–3.2
Protonymph	4.5	0.7	3.4–5.5

^a Calculations based on the mean duration in each of the 11 mite families.

microscope (magnification $16\times$) and the time they remained in the venter-to-venter mating position typical for mites of the family Parasitidae (Evans, 1992) was measured. After a pair separated, the mites were transferred to a plastic box to determine oviposition rates. The plastic boxes contained moist peat and food as before and were checked every 24 h. After each check, the mite pair was transferred into a new plastic box. The old box was kept to establish the number of eggs laid during the last 24 h. The females hid the eggs in the peat so the eggs could not be counted directly. Therefore the boxes were stored in the dark, the peat re-moistened daily, and the number of larvae that emerged in each box counted.

To estimate the duration of the life-cycle stages, 5 larvae of each mite pair were put into plastic boxes (1 box per family) equipped and kept as before. The containers were checked every day to record whether the mites had moulted.

At irregular intervals, the boxes used to induce adult moult and determine oviposition rates were observed under a dissecting microscope ($16\times$) for 1–2 min, and what the mites were feeding on was recorded. Additional observations on the feeding behaviour come from 3 similar boxes in which mites of all life-cycle stages were kept together.

RESULTS

Thirty-two of the 318 field-caught deutonymphs moulted into adults. Moulting was asynchronous; some deutonymphs moulted within 1 day after their introduction to the laboratory, others took up to 7 days. In total, 13 pairs of newly moulted adults were used for the mating experiments. In all pairs, mating started within 15 min after introduction to the test arena. Two pairs (mating duration 1.1 and 2 min, respectively) produced no offspring and therefore were discarded from further analysis. The 11 pairs that reproduced successfully remained in the mating position for an average duration of > 1 (Table 1). After separation, the male and female moved independently in the test arena and showed no obvious interaction.

All females started egg-laying within the first 24 h after mating and continued to lay eggs for several days (Table 1). The mean (\pm SD) number of eggs produced per female per day was: day 1 after mating, 5.5 ± 4.0 ; day 2, 14.5 ± 9.2 ; day 3, 15.7 ± 9.0 ; day 4, 16.1 ± 11.0 ; day 5, 13.7 ± 13.1 ; day 6, 11.9 ± 12.0 ; day 7, 9.8 ± 10.6 ; day 8, 7.2 ± 8.7 ; day 9, 3.6 ± 6.3 ; day 10, 1.7 ± 5.7 ; day 11, 1.6 ± 5.1 ; day 12, 0.6 ± 1.8 ; day 13, 0.4 ± 1.2 . All females lived for several days after they stopped laying eggs. Offspring development from oviposition to the emergence of the phoretic deutonymphal stage took 9.5 days on average (Table 1).

During the experiments adult females were often observed removing an individual grain from the pollen ball, rotating it between the chelicerae for a few seconds, discarding it, and returning to the pollen ball to fetch the next grain. Pollen grains processed in this way lost their normal bright yellow or blue colour and became pale and more translucent, indicating that the mites had removed and ingested the pollenkitt and nectar coating that covers the grain surface (cf. Royce & Krantz, 1989). Deutonymphs manipulated pollen in the same way, but no observations were made of larvae, protonymphs or adult males eating pollen. Larvae and protonymphs fed on the dead mealworm and on mite eggs. Adult males preyed on the larval and protonymphal instars. Once, a deutonymph ate another deutonymph.

DISCUSSION

Mites of the genus *Parasitellus* (previously *Parasitus*) hibernate in the deutonymphal stage and moult into adults after arriving in a bumblebee nest (Richards & Richards, 1976; Eickwort, 1994). In *P. fucorum*, mating occurred immediately after adult moult, as in other Parasitidae associated with nidicolous insects (Rapp, 1959; Korn, 1982; Schwarz & Walzl, 1996). Mating duration was extremely variable, from a few minutes to several hours. In the Parasitidae, mating usually takes < 10 min (Rapp, 1959; Costa, 1964; Zukowski, 1964; Schwarz & Walzl, 1996; Yasui, 1997). The extremely long mating times observed in *P. fucorum* may have been caused by males guarding females or applying mating plugs (Korn, 1982; Yasui, 1994). However, this does not explain why some of the matings observed were much shorter.

The oviposition rates and the duration of life-cycle stages determined for *P. fucorum* were within the range reported for parasitid mites colonizing insect nests (Costa, 1969; Schwarz & Walzl, 1996). Richards & Richards (1976) found much lower oviposition rates and a longer development in North American species of *Parasitellus*, but stated that this may have been due to sub-optimal rearing conditions. In *P. fucorum*, development from egg to deutonymph was completed in < 10 days and deutonymphs took a few days to moult into adults in the laboratory. Therefore, it is likely that *P. fucorum* produces several generations per colony-

cycle of the bumblebees. Multiple generations per colony-cycle were observed in North American species of *Parasitellus* (Richards & Richards, 1976). As *P. fucorum* deutonymphs can transfer between colonies by switching between foraging bumblebee workers (Schwarz & Huck, 1997), a short generation-cycle means that mites developing in a bumblebee nest can disperse to other nests and reproduce there within the same season.

It is known that in parasitid mites associated with insects, the adult moult of the phoretic deutonymph is triggered by feeding on the host's food resource or associated organisms (Pass, 1974; Wise, Hennessey & Axtell, 1988; Schwarz & Müller, 1992). Richards & Richards (1976) kept deutonymphs of *Parasitellus* with various foods, including a wax-pollen mixture from bumblebee nests, without observing any adult moult. In our experiments, deutonymphs moulted after feeding on fresh pollen collected by bumblebees, suggesting that freshly collected pollen is a necessary pre-requisite for moulting. Moulting success, however, was low, indicating that an additional stimulus may be necessary. Pollen also was the preferred food of adult females. The consumption of pollen by adult females and deutonymphs may have a negative effect on the bumblebees, which need the pollen as a food resource for their larvae. Males, larvae, protonymphs, and possibly deutonymphs, were predatory and oophagous in our study. In the field, bumblebee nests contain a variety of small arthropods, many of which are harmful to their hosts (Schmid-Hempel, in press), so the presence of oophagous and predatory mites could also benefit the host.

Acknowledgements

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Overwintering survival in relation to body mass in a field population of the wolf spider (*Hygrolycosa rubrofasciata*)

Janne S. Kotiaho*, Rauno V. Alatalo, Johanna Mappes and Silja Parri

University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FIN-40351 Jyväskylä, Finland

Key words: overwintering, survival, body mass, spider, *Hygrolycosa rubrofasciata*

INTRODUCTION

Body size is often considered to be an important trait affecting individual fitness. In arthropods, females commonly benefit from larger size directly through increased fecundity (Roff, 1992), and males through increased mating success (Andersson, 1994). It has also been suggested that larger individuals may in general have a better survival than smaller individuals (Calder, 1983; Peters, 1983). From this suggestion it may be predicted that during stressful environmental conditions larger individuals should do better than smaller individuals.

Overwintering of arthropods is one important environmental selective factor causing increased mortality. Under laboratory conditions the mortality of spiders increases with low winter temperatures (e.g. Almquist, 1970; Schaefer, 1977), and in the field overall mortality is high and affected by the severity of the winter (e.g. Huhta, 1965; Martyniuk & Wise, 1985; Schaefer, 1987; Gunnarsson, 1988). However, to understand how selection works on individual traits, studies at the individual level in natural populations are needed. Because studies of this kind are difficult to establish, they are rare. One example comes from a field experiment on overwintering survival of groups of small and large female *Pityohyphantes phrygianus* spiders (Gunnarsson, 1988). In this experiment, Gunnarsson did not find any evidence that the group of larger individuals would survive better than the group of smaller ones. However, in the same paper, Gunnarsson reports results from observational field studies that in some winters the population mean carapace width (a measure that does not change during winter) increased significantly in both sexes. This increase indicates that there was directional selection operating on size and favouring larger individuals. However, during other winters the population variance of carapace width in females decreased indicating that there may also be stabilizing selection on size (Gunnarsson, 1988). In another study with different stages of the spider *Linyphia marginata*, Martyniuk & Wise (1985) found no evidence that size differences within a stage affected winter survival. These studies suggest that

there may be directional or stabilizing selection on body size or no selection in relation to body size. However, implications that smaller individuals would do better than larger individuals are missing.

In this study, our objective was to determine whether the body mass of *Hygrolycosa rubrofasciata* (Ohlert) males was related to their overwintering survival, and to determine how overwintering affects the mass of the males in a field population.

MATERIALS AND METHODS

Hygrolycosa rubrofasciata is a small earth-dwelling wolf spider (Lycosidae) inhabiting open and moist meadows and bogs throughout the northern Europe. The study area in southern Finland is characterized by patchy cover of moss *Sphagnum* spp. and dry leaf litter, in which the spiders overwinter. In this area *H. rubrofasciata* overwinters once or twice in the pre-adult stage and finally as an adult. The body mass of adult males is highly variable ranging in this population from 9 to 25 mg (Kotiaho, Alatalo, Mappes & Parri, 1996). Between-male variation is much greater than within-male variation indicated by the high (82–99%) repeatability of male body mass (Kotiaho, Alatalo, Mappes & Parri, 1996). Generally, male body mass has not been found to be related to survival of the individuals (Kotiaho, Alatalo, Mappes & Parri, 1996), but under simultaneous food deprivation and an experimental increase of the sexual display rate, larger males have been observed to have a slight survival benefit compared to smaller males (Mappes *et al.*, 1996).

During 1 and 2 September 1996 males were captured with round plastic pitfall traps (diameter 40 mm) and by hand from a small (*c.* 30 × 40 m) bog at Sipoo, Southern Finland. At this time males have already moulted to adults. All captured males were marked with a combination of 3 small coloured paint dots on the dorsal surface of the abdomen. Males were weighed to the nearest 0.1 mg and finally released within 24 h from capture. All males were released from the same location of the bog.

Starting from 28 April 1997 males were recaptured in pitfall traps and by hand from the same bog in Sipoo. The pitfall traps were arranged in a grid constructed of 20 rows separated by *c.* 50 cm, with 20 pitfall traps

*All correspondence to current address: J. S. Kotiaho, Department of Zoology, University of Western Australia, Nedlands, WA 6009, Australia. E-mail: jkotiaho@cyllene.uwa.edu.au

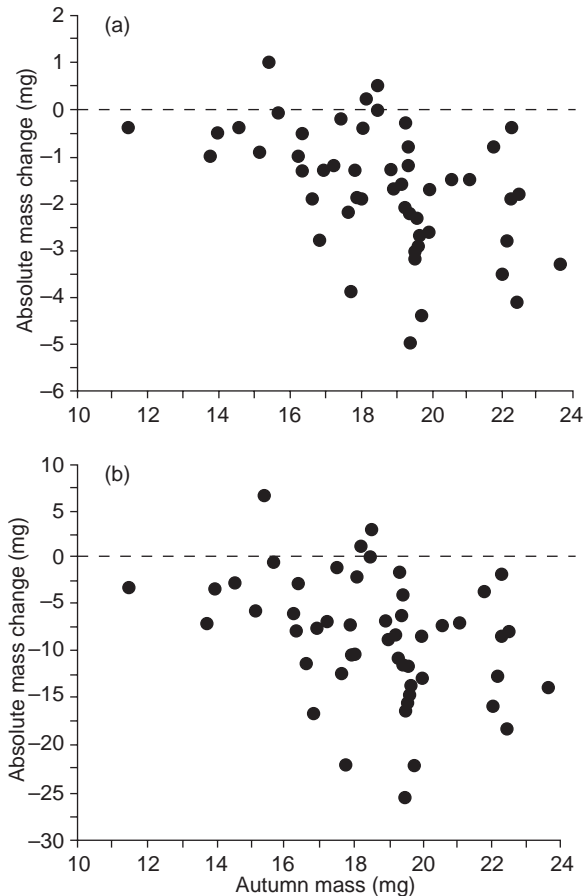


Fig. 1. Scatter plot of autumn body mass and (a) absolute body mass change of survived males and (b) relative body mass change of survived males.

c. 50 cm apart in each row. The point where males were released in previous autumn was the centre of the grid of pitfall traps. After a few days the grid was enlarged to cover an area *c.* 20 × 20 m around the releasing point. On 17 May 1997, searching for males was terminated because of the cessation of the capture of marked individuals in pitfall traps. All captured males were identified by their colour combination and weighed to the nearest 0.1 mg.

RESULTS AND DISCUSSION

In the autumn 286 males were caught, marked, weighed and released. In the spring we recaptured a total of 63 marked males, nine of which died before they could be measured. The body mass of the remaining 54 males averaged (\pm SD) 18.39 \pm 2.56 mg in autumn and 16.91 \pm 2.18 mg in spring. The seasonal difference in body mass was significant (paired *t*-test $t=9.39$, d.f. = 53, $P < 0.001$) and was the result of most males losing mass during winter (mean \pm SD mass change was -1.64 ± 1.28 mg). There was also a strong and highly significant positive correlation between male body mass in autumn and in spring ($r=0.853$, $n=54$, $P < 0.001$). This correlation indicates that body mass in spring is

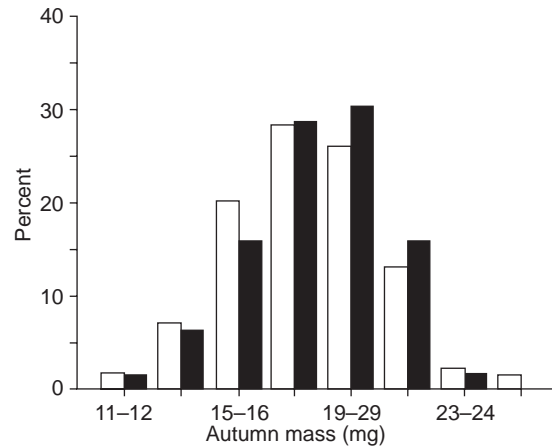


Fig. 2. Frequency distribution for the autumn mass of males surviving (closed bars) and not surviving (open bars).

largely dependent on the initial body mass in autumn. However, when we compared the absolute mass change during winter to the body mass in autumn there was a negative relationship indicating that larger males lost more mass ($r = -0.459$, $n = 54$, $P < 0.001$) (Fig. 1a). It may be that a negative correlation results if larger males need to spend absolutely more resources to maintain the vital functions of their larger body during winter. However, this assumption had to be discarded after comparison of relative mass change to the body mass at autumn; there was still a significant negative relationship indicating that larger males lost more mass per unit body mass during the winter than smaller males ($r = -0.345$, $n = 54$, $P = 0.011$) (Fig. 1b). This larger mass loss per unit mass suggests that large males suffer increased energy expenditure as a result of their size during overwintering.

However, there was no difference in the autumn mass between males who survived and males who did not survive (Fig. 2) (mean \pm SD 18.54 \pm 2.41 mg and 18.35 \pm 2.60 mg, respectively; two-sample *t*-test $t=0.52$, d.f. = 284, $P = 0.604$). The directional selection differential (*I*) may be calculated as the difference between mean body mass of those who survived (X_s) and mean body mass of the initial population (X_p) divided by the standard deviation of the initial population (SD_p); $I = X_s - X_p/SD_p$ (Endler, 1986). In this case directional selection differential was +0.058 for larger size and the true estimate with 95% confidence (Zar, 1996) falls between -0.20 and $+0.35$. Thus, directional selection is not significantly different from zero, as indicated also by the two-sample *t*-test above. Variance selection or the stabilizing/disruptive selection differential (*C*) may be calculated as the difference between variance in those who survived (v_s) and the variance of the initial population (v_p) divided by the variance of the initial population:

$$C = v_s - v_p/v_p \quad (\text{Endler, 1986})$$

In this case the selection differential was -0.112 and the true estimate with 95% confidence (Zar, 1996) falls between -0.35 and $+0.27$. Since the estimate was nega-

tive it was stabilizing selection. However, this differential is also not significant as the confidence intervals include zero and the population variance ratio test is not significant ($F_{222,62} = 1.16$, $P = 0.242$). These analyses clearly demonstrate that the body mass of the males is not an important determinant of overwintering survival.

The most important finding of this study was that there was no detectable effect of male body mass on their overwintering survival. Because of the moderately large sample size, this result is robust and we can be confident in accepting the null-hypothesis that mass has no great impact on overwintering survival. However, this study concentrated only on adult males and thus any differential mortality in juvenile stages remains to be tested. Interestingly, however, larger males lost proportionally more mass than smaller males. This suggests that large males may have an additional energy expenditure because of their large body mass while overwintering. However, in optimal conditions, the per unit mass energy consumption of males is not related to their body mass (Kotiaho, in press; Kotiaho, Alatalo, Mappes, Nielsen *et al.*, in press). Thus, while under optimal conditions there is no difference in the energetic requirements of small and large males, it seems that under harsh environmental conditions, such as cold and long winters, larger males may have an increased energy expenditure compared with smaller males. Nevertheless, this increased energy consumption does not manifest itself through differential overwintering mortality, but rather, it seems that large males can afford to expend more energy than smaller males. This is supported by an earlier study (Mappes *et al.*, 1996) where it was found that when energy availability is controlled and males are stressed, large males have a small but significant survival advantage compared with smaller males. This indicates that larger males may have proportionally larger energy reserves and may be able to spend more energy before they are exhausted compared with smaller males.

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Skeletons in the cupboard? Quantifying bird predation on Atlantic salmon: atlas vertebra: fish length equations revisited

D. N. Carss and M. Marquiss

Institute of Terrestrial Ecology, Hill of Brathens, Glassel, Banchory, Kincardineshire AB31 4BY, Scotland

INTRODUCTION

Throughout Europe there is considerable concern about the potential impact of sawbill ducks *Mergus* spp. and

great cormorant *Phalacrocorax carbo* on catches of commercial fish (reviews by Marquiss & Carss, 1994; Russell *et al.*, 1996). A prerequisite to estimating impact is to quantify the consumption of commercially impor-

tant fish by birds. This requires site-specific data on (1) bird numbers, (2) their daily food intake and (3) diet. Considerable effort has been directed at quantifying (2) and (3) and exploring the biases associated with different methods (see Carss *et al.*, 1997 for review).

One commonly used method of diet assessment involves the analysis of stomach contents using specific 'key bones' to identify fish species and estimate their lengths (Carss *et al.*, 1997). The use of key bones to estimate the sizes of fish in bird stomachs eliminates the major bias against small, rapidly digested fish which results from using the lengths of only intact fish from stomachs (Marquiss & Carss, 1997). Fish length estimates derived from key bones are easily converted to biomass estimates using appropriate length:weight relationships and diet, then assessed as percentage biomass for each prey species reconstituted from stomach samples of different provenance (e.g. Carss & Marquiss, 1997).

The first ('atlas') vertebra has been used to differentiate Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* and to estimate (95% C.I. ± 10 mm) their lengths (Feltham & Marquiss, 1989). However, the use of the Feltham & Marquiss (1989) atlas bone:fish length equation has been criticized (Armstrong & Stewart, 1996, 1997a) as systematically underestimating the length of salmon smolts consumed by birds. As juvenile salmon change from parr to smolt before their migration to sea, their bodies elongate; for wild fish, of any given atlas width, smolt are longer than parr by about 11 mm (Armstrong & Stewart, 1997b). Although the Feltham & Marquiss (1989) equation was derived from an unknown mixture of parr and smolts, it was closer to Armstrong & Stewart's regression for parr than for wild smolt. Thus, if smolt predominated in the diet, their average length would be underestimated, resulting in some small smolt being misclassified as parr on the basis of estimated length (e.g. Feltham, 1995).

There is currently no way of classifying fish as smolt or parr from the partially digested remains of most of the salmon in stomachs, so it is not possible to apply the wild smolt and parr equations of Armstrong & Stewart (1996) separately. The only way to derive an overall equation for atlas width to fork length, applicable to all juvenile salmon atlases from the stomachs of predators, is to use the most pristine of whole fish recovered from these same stomach samples. This note investigates the validity of this approach in relation to the original equation proposed by Feltham & Marquiss (1989) for three species of fish-eating bird and discusses recent criticism of this method and its application.

METHODS

Pristine, intact Atlantic salmon were removed from the stomachs of goosanders *Mergus merganser*, red-breasted mergansers *Mergus serrator* and great cormorants shot under licence on Scottish rivers by fisheries managers

and forwarded to the Institute of Terrestrial Ecology for analyses. These salmon, presumably swallowed immediately before the bird was shot, showed no visible signs of digestion and had intact tail and fin rays. The fork lengths of these fish were measured to the nearest mm, then the atlas vertebrae digested out with biological washing powder, and fork width measured to the nearest 0.125 mm. These fish had been frozen for over a year so we assumed that they had shrunk during freezing (Armstrong & Stewart, 1997b). We estimated their original fork length (FL_{live}) using a regression derived from wild juvenile salmon ($n=27$, FL range = 39–113 mm) that had been measured live, killed and then frozen for 18 months, thawed and remeasured (FL_{frozen}):

$$FL_{\text{live}} = 1.980 + 1.032.FL_{\text{frozen}}$$

($R^2 = 0.998$, $P < 0.001$, 95% C.I. for slope: 1.028–1.036).

The estimated original fork lengths of fresh salmon from bird stomachs were then regressed on atlas width and compared with the Feltham & Marquiss (1989) and Armstrong & Stewart (1996) equations. The revised atlas width:fish length equation derived in the present study was then used to estimate (a) the numbers and sizes of fish consumed by fish-eating birds, (b) the number of salmon consumed per 100g of reconstituted stomach contents (the precursor to estimating the intake rate of salmon by birds (see Marquiss *et al.*, 1998), from samples from Scottish rivers. These assessments were then compared with those made using Feltham & Marquiss' (1989) original equation to quantify the influence of the revised equation. In order to make these comparisons, samples of stomachs were chosen which (a) had the highest estimated salmon component in the reconstituted diet, these were 'individual' samples ($n=13$) for a particular bird species, river, season and year and (b) included those samples in (a) as 'combined' samples ($n=9$) for particular bird species, river, season and all years for which data were available.

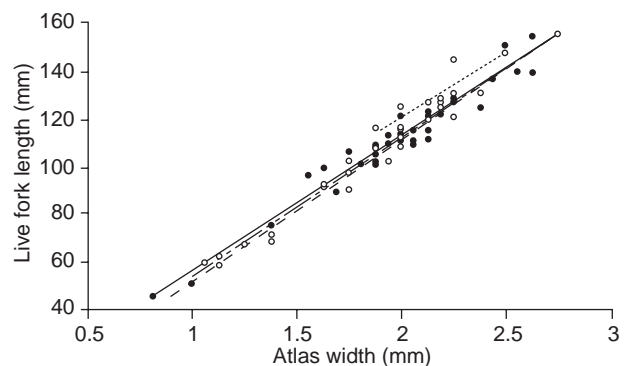


Fig. 1. Regression of fork length (L_F) on atlas vertebra with (W_V) of salmon from bird stomachs in winter (●) and spring (○) ($L_F = 59.5 W_V - 5.01$, $R^2 = 0.942$) in comparison with published regression lines: present study (—), F & M (1989) (---), A & S (1996) parr (-.-.-) and smolt (.....).

Table 1. Regression equations of salmon fork length (FL) on atlas width (FVW)

Provenance	Sample	Gradient	Intercept	<i>n</i>	<i>R</i> ²
Feltham & Marquiss (1989)	Parr and smolt	60.5	-8.95	88	0.961
Armstrong & Stewart (1996)	Parr	57.1	-3.47	29	0.971
Armstrong & Stewart (1996)	Wild smolt	56.9	+7.97	20	0.755
Present study	Parr and smolt from bird stomachs	59.5	-5.01	82	0.942

Table 2. The proportion by biomass of total reconstituted stomach contents (B), using the Feltham & Marquiss (1989) atlas width:fish length equation (F&M) and that derived in the present study (P). Difference = value calculated as present study - F&M (1989) value

Bird species	River	Month, year	Salmon % of total B		Difference (%)
			F&M	P	
Goosander	Beaully	Mar/Apr, 1991	62	63	+1
	Beaully	Mar/Apr, 1995	58	58	0
	Dee	Oct-Dec, 1995	55	56	+1
	Deveron	Mar, 1992	54	55	+1
	Deveron	Mar/Apr, 1994	56	57	+1
	Spey	Apr, 1993	51	52	+1
	Spey	Apr, 1996	76	76	0
Red-breasted mergansers	Conon	Apr, 1995	62	63	+1
	N. Esk	Mar/Apr, 1995	53	56	+3
	S. Esk	Apr, 1993	53	55	+2
Cormorant	Deveron	Oct-Dec, 1992	8	9	+1
	Tweed	Feb/Apr/Jun, 1991	7	7	0
	Tweed	Apr, 1992	16	16	0

Table 3. The number of salmon per 100g of reconstituted stomach contents calculated using the Feltham & Marquiss (1989) atlas width : fish length equation (F&M) and that derived in the present study (P). Difference = value derived from F&M (1989) minus that from present study/F & M derived value as percentage

Bird species	River	Season	Total no. salmon	No. of salmon per 100g		Difference (%)
				F&M	P	
Goosander	Beaully	Mar/Apr	54	7.01	6.85	2.28
	Dee	Dov/Dec	356	5.11	5.04	1.19
	Deveron	Mar/Apr	117	5.52	5.44	1.45
	Spey	Mar/Apr	94	5.06	5.00	1.37
Red-breasted mergansers	Conon	Mar/Apr	30	7.46	7.18	3.75
	N. Esk	Mar/Apr	158	8.27	7.93	4.11
	S. Esk	Mar/Apr	147	8.35	8.10	2.99
Cormorant	Deveron	Nov/Dec	51	0.40	0.39	2.50
	Tweed	Mar/Apr	106	0.42	0.42	-

RESULTS

Pristine salmon comprised <4% of the fish recovered from stomachs, but a diverse sample of 82 fish was collected from the stomachs of all three species of birds, from 10 Scottish river systems over 5 years (1992-1995), and two seasons (winter and spring).

There were no significant differences between the gradients or intercepts of regression slopes for winter and spring samples, so the data were combined to produce an overall regression equation for original fork length on atlas width (Fig. 1). This was similar to that of Feltham & Marquiss (1989) but differed markedly

from that given for wild smolt by Armstrong & Stewart (1996) (Table 1). These authors' regressions for parr and wild smolt had lower gradients than did the regression lines of Feltham & Marquiss, and the present study.

Generally, the diet of fish-eating birds on northern Scottish rivers is less diverse with a greater proportion (by biomass) of salmon than on southern ones (Marquiss *et al.*, 1998). Overall (Table 2), the highest proportions (>50% biomass) of salmon were recorded from samples from the rivers Beaully, Dee, Deveron, Spey (goosanders, *n* = 7 samples), Conon, North Esk and South Esk (red-breasted mergansers (*n* = 3 samples). Lower proportions of salmon were recorded

in cormorant stomachs, the highest (9–16% biomass) being in samples ($n = 3$) from the rivers Deveron and Tweed.

Using the atlas:fish length equation derived in the present study resulted in higher biomass estimates for salmon than those which were derived using Feltham & Marquiss' (1989) original equation. Salmon biomass estimates were increased by 6–53 g which resulted in small changes in the relative contribution of salmon to the reconstituted diet: no change in four samples, 1% increase in seven samples and 2% and 3 % increase in one sample each (Table 2).

Using the atlas:fish length equation derived in the present study resulted in lower estimates of the number of salmon per 100 g of reconstituted stomach contents than those which were derived using Feltham & Marquiss' (1989) original equation. Estimates decreased by 0–0.34 salmon per 100 g, reducing the estimated intake of salmon per 100 g by 0–4.1 % (average = 2.2%) as determined using the Feltham & Marquiss (1989) equation (Table 3).

DISCUSSION

Armstrong & Stewart's (1996) regressions for parr and wild smolt had lower gradients than did the regression lines of Feltham & Marquiss (1989) and the present study; consistent with the hypothesis that these latter two regressions were derived from samples of juvenile salmon that were predominantly parr but contained a few large fish that were elongate and therefore probably smolts.

The regression equation derived directly from whole fish from stomachs is so similar to that of Feltham & Marquiss (1989), it is unlikely that the lengths of most juvenile salmon in bird stomachs had been systematically underestimated leading to their misclassification as parr instead of smolt (c.f. Armstrong & Stewart, 1996). Nevertheless, it is clear from the slightly steeper gradient that at least a few smolts must have been included in our sample of 83 whole fish from stomachs. At present there is no method to classify most of the larger juvenile salmon from bird stomachs as parr or smolt so we cannot yet apply separate regression equations to estimate their fork length from the width of atlases.

The equation derived in the present study from intact fish from stomachs is now the most appropriate that is available. However, this does not mean that previous studies based on the original Feltham & Marquiss (1989) equation are misleading. In the present samples, use of the Feltham & Marquiss (1989) equation underestimated the relative contribution of salmon to the diet of fish-eating birds by no more than 3% of the biomass of reconstituted stomach contents and usually by 1% or less. Furthermore, use of this equation overestimated the intake of salmon (i.e. the number of salmon consumed per 100g of reconstituted stomach contents) by no more than 3–4% (average 2.2%).

Nevertheless, there are still some reservations about

the 'global' use of the atlas: fish length equation derived in the present study because the samples we used were too small and too disparate to search for variation associated with provenance. Future work might measure increased numbers of intact fish to examine variation in the gradients of regression lines specific to bird species, river system and time of year. With larger samples, separate equations might be derived that would improve precision, though only appropriate to samples of specific provenance.

To date, much emphasis has been placed on estimating the size and, by implication, the status (i.e. parr or smolt) of Atlantic salmon in the diet of fish-eating birds. However, the refinements which can be applied to salmon atlas measurements from bird stomachs are equally likely to hold for some brown trout too, as presumably the physical changes involved in smolting are similar for migratory brown trout, as are the differing consequences of bird predation on trout of different status.

Finally, while methodological refinements to techniques that estimate the size, and status, of fish in the diet of predators are to be welcomed, they must be kept in perspective. Such refinements must be seen against a background of the huge variability often associated with current fisheries assessments, including those of salmon in freshwaters. Many of the fish population parameters necessary to model accurately the potential impact of piscivorous predators (e.g. the density of presmolt salmon in Scottish rivers, Marquiss *et al.*, 1998) are currently of unknown accuracy. Similarly the use of 9 cm as the nominal size-discriminator between salmon parr and smolts by Feltham (1990, 1995) is a consequence of the lack of more useful published data. This value was chosen as it was the minimum length of salmon smolts on the River North Esk, which are tagged and measured during downstream migration to the estuary and therefore fish longer than this could be smolts (Feltham, 1990). Finally, it is worth reiterating (cf. Carss *et al.*, 1997) that even when data are sufficiently rigorous to quantify the consumption of commercially important fish such as Atlantic salmon, the question of whether or not such consumption affects the commercial catches of these fish is still unanswered.

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