The effect of body size on the outcome of fights in burying beetles (*Nicrophorus*)

Merja Otronen

In *Nicrophorus* beetles several individuals arrive at a carcass but usually only one pair stays and breeds there. To find out how the breeding pair is selected, intra- and interspecific fights and intersexual interactions in three *Nicrophorus* species (*N. vespilloides*, *N. investigator* and *N. vespillo*) were studied. The likelihood of different kinds of fights was estimated by using the abundance, habitat preference and seasonal occurrence of the species. In intraspecific fights large individuals won against smaller ones in all species, and in *N. vespilloides* the arrival time was also important. In interspecific fights individuals belonging to the two largest species had an advantage over the smallest species, even when they are the same size as their opponent. No mate choice was observed; the breeding pairs at carcasses are simply the winners of intrasexual fights. While burying the carcass the male and female often learn to recognize each other and behave aggressively towards intruders.

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1. Introduction

During their lifetime animals may experience many different conflict situations. A successful behavioural strategy is well adapted to its environment and should also be adaptive in conflict situations with conspecifics and even with heterospecifics (Riechert & Hammerstein 1983). A game theoretical approach to animal conflicts is to seek an evolutionarily stable strategy, such that if all individuals in a population adopt this strategy it cannot be invaded by any alternative strategy (Maynard Smith & Parker 1976).

Predictions derived from various game theoretical models have already been tested in many species. For example, it is possible to examine the importance of three kinds of asymmetries in animal conflicts (Maynard Smith & Parker 1976, Hammerstein 1981, Parker & Rubenstein 1981, Maynard Smith 1982). The resource-holding potential asymmetry (RHP), like the size or the fighting ability of an individual, is important in conflicts in many species (Davies & Halliday 1978, Riechert 1978, Sigurjonsdottir &

Parker 1981, Otronen 1984, Thornhill 1984). The payoff asymmetry, which measures the relative costs and benefits for the contestants can also affect the outcome of conflicts in various species (Riechert 1979, Sigurjonsdottir & Parker 1981, Krebs 1982). The third asymmetry, ownership, is a role asymmetry and its significance has been more difficult to study because it is often connected with the other asymmetries, for example, owners are usually bigger and have more to gain (but see Davies 1978).

In this paper, I report on individual conflict situations in three species of *Nicrophorus* F. beetles fighting for small carcasses which they use for breeding (see below). I wanted to find out which individuals had an opportunity to stay and breed at a carcass and why these individuals were successful. Conflict situations in *Nicrophorus* are particularly interesting because several species may visit the same carcass and both intra- and interspecific fights are possible. Furthermore, natural conflict situations in *Nicrophorus* are complicated by the fact that both males and females fight. In this study, the importance

of individual size was studied in both intra- and inter-specific conflicts. In addition, the effect of arrival time was tested for intraspecific conflicts. To find out how breeding pairs are formed intersexual inter-actions were studied. Some ecological data was col-lected as background information on the frequency of different conflict situations.

The burying and breeding behaviour of *Nicrophorus* beetles has been described by several authors (Fabre 1899, Pukowski 1933, Milne & Milne 1976). In the more recent works, competition between spe-cies and individual interactions in the field have been studied in more detail in England (Easton 1979) and in North America (Wilson et al. 1984, Wilson & Fudge 1984). After finding a small carcass *Nicro-phorus* beetles start to bury it in the ground, several individuals working at the same time. The final ownership of the carcass, however, is settled during conflicts and very often only one pair, a male and a female, stays and breeds at the carcass. During the burial process the corpse is carefully worked into the shape of a ball. After the burial the female lays her eggs in a burrow alongside the ball, and then after hatching the larvae move to the carcass. Feeding together, the larvae consume the carrion ball from inside so that in the end only a thin shell is left behind. During larval development the female (sometimes accompanied by the male) stays at the carcass taking care of the food ball and the larvae. The female leaves the nest only after the larvae pupate.

2. Material and methods

The study was conducted at the Lammi Biological Station in southern Finland during the summers of 1983 and 1984.

Beetles captured in nature

Beetles were captured with 'live capture' pit-fall traps (Pukowski 1933) made of plastic containers (14×11×10 cm). Two cm of soil and a bait of fish was placed on the bottom of a container and it was covered with a lid. In the lid there was a hole of about 3.5 cm in diameter, and a plastic tube (3.5 cm long) was placed into this. The tube was used to prevent beetles from escaping once they had entered the container (the tube was too narrow for beetles to fly through and too smooth for them to climb up). The containers were buried at ground level.

To obtain information on the seasonal occurrence and habi-tat preferences of different species, trapping was carried out in five periods in 1983 (4–6 June, 1–5 July, 25–29 July, 17–19 August and 3–6 September) and four periods in 1984 (15–18 May, 29 May–2 June, 10–14 July and 2–6 August). Beetles were trapped in three habitats: pasture, deciduous forest and spruce forest. Each trapping period lasted for four days and collections

were made daily. In some results the last trapping period in September 1983 has been excluded because it contained indi-viduals which had just emerged (according to Pukowski (1933), *N. vespilloides* and *N. vespillo* hibernate as an adult).

The same containers as above were used to capture breeding pairs in nature. For this experiment the traps were filled with soil, and a fish bait (15 to 20 g) was placed on them. They were buried at ground level and left open in the expectation that beetles would arrive and bury the bait. The traps were checked after 24 hours and beetles were collected if the bait had totally disappeared from sight. Fifteen traps were used at the same time and the distance between traps was always over 100 m. The experiment was repeated three times in July 1984 on an area 3 km away from the main trapping area.

Laboratory experiments

Individuals captured alive were used in laboratory experi-ments on intra- and interspecific interactions. Individuals were sexed on the basis of the shape of the tip of their abdomen, weighed and the length of their elytra along the middle was measured. The experiments were conducted in plastic containers (30×25×10 cm) with 5 cm of soil and a piece of fish meat (about 15 g) on the bottom. Before starting the experiments the fish meat was kept in a warm place for 24 hours. *Nicrophorus* is known to use many kinds of corpses, for example, small mam-mals, small birds, reptiles and amphibia (Elton 1966). Therefore, although fish may not be very common carrion type for *Nicrophorus*, it is not likely that this would affect individual behaviour. Burial of fish left in nature was frequently observed during the study. The laboratory was darkened and the temperature in the room varied from 21 to 25°C. All experiments were started at 8 a.m. Although the *Nicrophorus* species used in this study have been reported to be nocturnal, there is observational evidence that after finding a carcass beetles are active until it is buried, regardless of the time (Pukowski 1933, and pers. obs. by the author). In the experimental containers, in the darkened laboratory, all individuals were active during the day.

Experiments on intra- and interspecific conflicts

In intraspecific experiments two marked males and females were released near the carcass. Two different experiments were conducted. To study the importance of body size, four indi-viduals (two males and two females) of different size were released in the container at the same time and after 12 hours the pair at the carcass was identified. The second experiment was conducted to find out the importance of early arrival. In this experiment, individual size was controlled, namely, the two males and the two females released in the container were of the same size. One pair was released near the carcass first and it started burying within an hour. The second pair was released near the carcass 4 to 5 hours later and finally, after 12 hours from the beginning of the experiment, individuals found at the carcass were identified. In both experiments the length of elytra was used to measure individual size.

In the interspecific experiments only the importance of in-dividual size was studied. The experiments were done in a sim-ilar way to the corresponding intraspecific ones, except that the two pairs released in the container belonged to different species.

Table 1. Differences in fresh weight and elytra length in *Nicrophorus* beetles. The first part of the table gives the median of elytra length for males and females in each species and the *z*-values (Mann-Whitney *U*-test) show the difference between sexes. The second part gives *z*-values in the interspecific comparisons of fresh weight (see Fig. 1 for the distribution of fresh weight in these species). All *z*-values in the second part are significant (*P*<0.001). The number of individuals is given in parentheses.

1) Elytra length (mm):

	Males	Females	z	P
N. vespilloides	7.8 ± 0.7 (430)	8.0 ± 0.7 (461)	5.23	0.001
N. vespillo	8.6 ± 1.1 (83)	8.6 ± 1.0 (57)	0.04	NS
N. investigator	9.4 ± 1.1 (129)	9.9 ± 1.1 (123)	2.69	0.01

2) Mann-Whitney *U*-test on the difference in fresh weight between species:

		Fresh weight (g)	N. vespilloides		N. investicator	
			Males (223)	Females (189)	Males (136)	Females (133)
N. vespilloides	males	0.196 ± 0.061	–	–	–	–
	females	0.183 ± 0.049	–	–	–	–
N. vespillo	males (79)	0.275 ± 0.078	6.98	6.06	4.16	5.34
	females (60)	0.272 ± 0.096	6.46	5.43	3.82	4.85
N. investigator	males	0.324 ± 0.109	12.42	11.57	–	–
	females	0.352 ± 0.092	13.25	12.56	–	–

Also, body weight was used to measure individual size. Fresh weight was preferred for the length of elytra because the species are of a slightly different shape. Comparison of fresh weights may not be totally satisfactory either because an individual's weight may vary according to the gut content or the reproductive state in the case of females.

In all experiments, to ensure that the losing beetles were willing to bury the carcass, the winners were removed and the losers were left alone in the container. Only those experiments in which the losing pair buried the carcass when left alone have been taken into account in interspecific results. In intraspecific experiments a result has been included in male-male interactions, even if only one of the females was active. In all experiments individuals were regarded as being active if they were found under the carcass or burying it.

Mate choice experiments

To study mate choice one pair was allowed to stay together at the carcass for 3 to 4 hours. Then either the male or the female was separated by placing a glass tube over it. Two new potential mates were introduced separately to the remaining individual. One of the new mates was smaller and the other larger than the original mate. When introducing the new mates the order of introducing a large and a small mate was altered in every second experiment. The acceptance or rejection of the new mates was recorded.

Rearing experiments

Females of known size were used in the rearing experiments (length of elytra 8, 9, 10 or 11 mm). Females were given a carrion of either 3.5, 5, 10, 15 or 20 g and a male of medium size,

and were allowed to lay eggs and rear the larvae. The number of last instar larvae was counted and the weight of each pupa was measured.

3. Results

3.1. Intra- and interspecific size variation

Nicrophorus beetles have a large size variation within species (Fig. 1) which makes them very suitable for studying the effect of size in individual conflicts. In all three species the coefficient of size variation is 25% or more, both in males and females. Comparing elytra lengths of males and females within species, females are significantly larger than males, on average, in *N. vespilloides* and also in *N. investigator* (see Table 1). In the third species, *N. vespillo*, the size difference between males and females is not significant.

In spite of the fact that the minimum weight was very similar in all species studied and their size distributions overlap (Fig. 1) it was possible to distinguish a small, a medium-sized and a large species. Of the three species, *N. vespilloides* was the smallest species, *N. vespillo* the middle sized species and *N. investigator* the largest one. The difference in size between the species is statistically significant (Table 1).
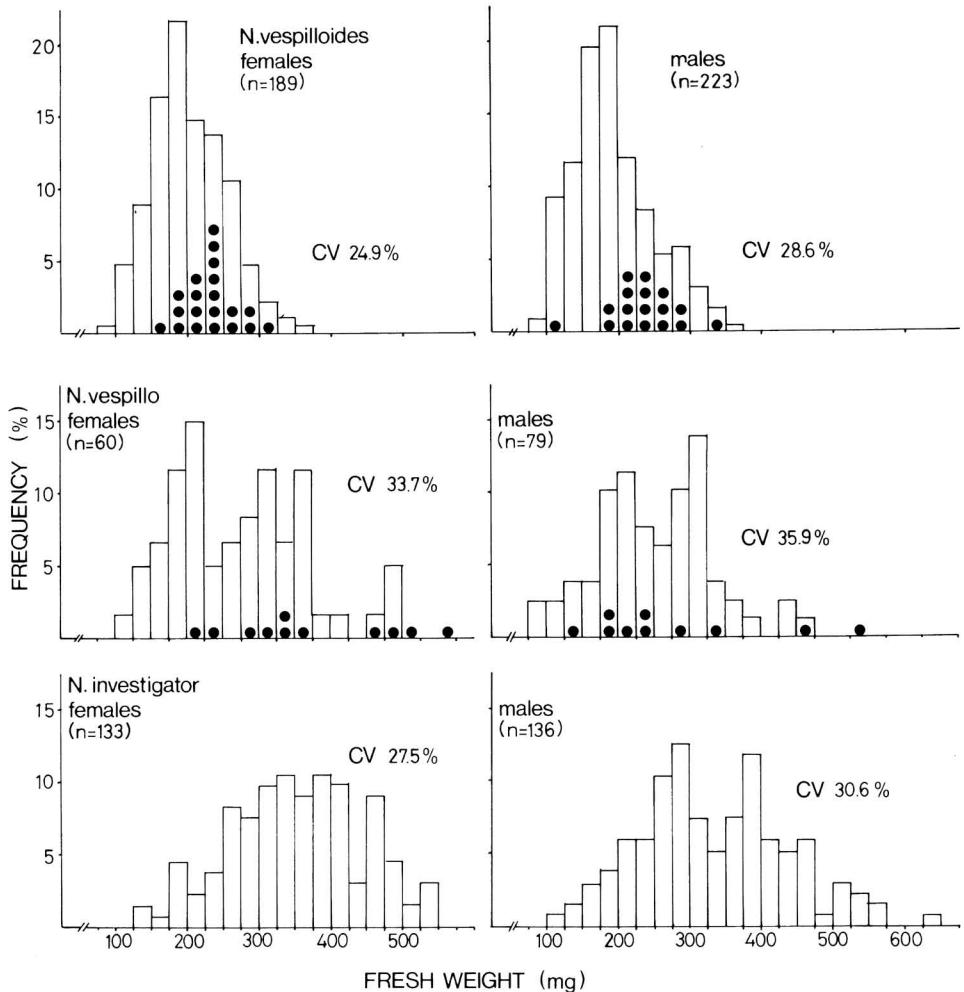
Fig. 1. Size distribution in the three *Nicrophorus* species and the size of individuals found in pairs in nature. The fresh weights (mg) of females and males are plotted separately and the number of observations and the coefficient of variation are given. Circles inside the columns in *N. vespilloides* and *N. vespillo* indicate individuals which were found in pairs in nature. See Table 1 for statistics.

3.2. The likelihood of intra- and interspecific conflicts

In the study area the most common species was *N. vespilloides*, 77% and 66% of the captured individuals belonging to this species in 1983 and 1984, respectively. The next species was *N. investigator* with 19% in both years and the rarest species was *N. vespillo* with 4% and 14% of the captured individuals (pooled data from the first four collection periods in 1983, $n=429$ and from the four collection periods in 1984, $n=351$).

The habitat differences between species were significant (Table 2). According to my data, *N. vespilloides* occurs in deciduous and spruce forests. *N.*

Table 2. The percentage frequency of the three *Nicrophorus* species found in the studied habitats. The difference in habitat distribution between species is significant ($\chi^2=428.33$, $df=4$, $P<0.001$).

	Deciduous forest	Field	Spruce forest
N. vespilloides	59.5 (443)	4.7 (35)	35.8 (266)
N. investigator	28.7 (43)	51.3 (77)	20.0 (30)
N. vespillo	8.3 (6)	86.1 (62)	5.6 (4)

investigator occurs in fields but it is also found in deciduous and spruce forests quite frequently. *N. vespillo* occurs almost exclusively in fields.

Wilson & Knollenberg (1984) have suggested that pit-fall trap results give a biased estimate of the community because they are not equally attractive to all individuals. In particular, they found that actively reproducing individuals avoided their traps. In this study, the condition of ovaries in the captured females was not checked. However, no biased sex ratio was found in any of the species which could have indicated the absence of reproducing females. The proportion of males was 53%, 47% and 48% in *N. vespilloides*, *N. vespillo* and *N. investigator*, respectively (each trapping period was tested separately and in none of them was the sex ratio significantly different from 50:50).

How often do *Nicrophorus* beetles encounter each other at a carcass? In my traps the average number of individuals found daily in a trap varied, being 2.7 in deciduous forests, 1.7 in spruce forests and 0.9 in fields. Since the burial of a carcass can take up to 24 hours (Wilson & Knollenberg 1983, pers obs.), interactions between individuals are likely at most of the carcasses in nature. However, pit-fall trap captures are not a very good method of estimating absolute encounter rates. For example, many extra carcasses are introduced into each habitat and trapped individuals are not returned back into the community. Therefore, the above estimates are likely to be much lower than at carcasses in natural circumstances.

In the following, information on the abundance, habitat and seasonal occurrence of the species has been used to estimate the probability that an individual encountered at a carcass is a conspecific or non-conspecific (Fig. 2). The lines in the figure indicate the proportion of individuals belonging to each species, in each habitat, during the summer and give the likelihood of an intraspecific encounter. It should be noted that only about one half of intraspecific encounters are intrasexual and therefore likely to result in a conflict. The space above the lines shows the likelihood that the two individuals at the carcass belong to different species and it is assumed that in these encounters there is always a conflict between individuals. Obviously, the use of only three niche dimensions when assessing the likelihood of an interspecific encounter will give only a rough estimate. To obtain a better estimate, several other dimensions, for example, temperature and diurnal activity (see Wilson et al. 1984) should also be included.

In *N. vespilloides* most of the encounters during the summer are likely to be conspecific and the probability of an interspecific encounter is very small in the two habitats, deciduous forest and spruce forest,
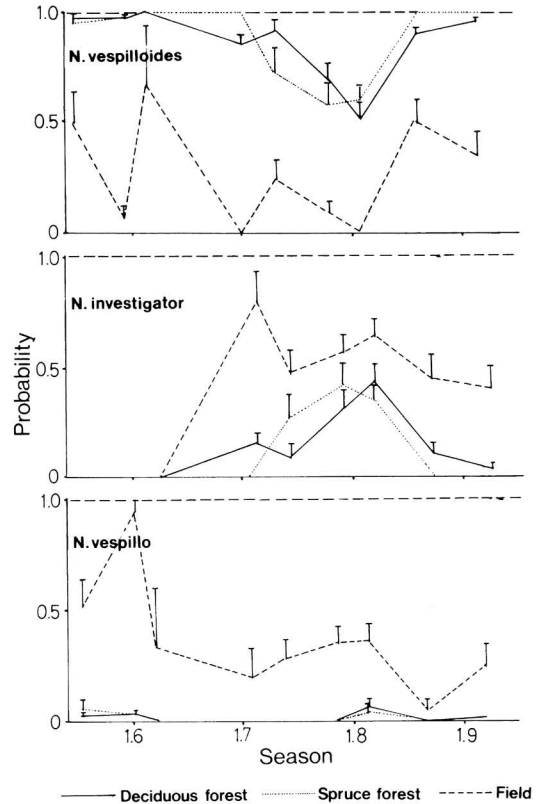

Fig. 2. Likelihood of intra- and interspecific encounters in *Nicrophorus*. The lines show the probability that an individual encountered in different habitats is a conspecific when the abundance and seasonal occurrence of the species are taken into account. Each point on the line contains information from four trapping days and the binomial variance for the trapping days is given. The space above each line indicates the likelihood that the individual encountered belongs to another species.

where this species mainly occurs. The likelihood of an interspecific encounter increases towards the end of July and the beginning of August, and during this period the likelihood of an interspecific conflict actually exceeds that of an intrasexual one. In *N. investigator* intraspecific encounters are slightly more likely in fields, in its main habitat, but otherwise interspecific encounters prevail (note that this species starts flying later than the two other species). In the rarest species, *N. vespillo*, besides a short period at the end of May, interspecific encounters are more likely than intraspecific ones throughout the summer in all habitats. In addition, the small likelihood of intraspecific encounters in *N. vespillo* indicates that this species may have difficulties in finding a mate, in particular, when away from its main habitat.

Table 3. The importance of size in intraspecific conflicts in *Nicrophorus*. The larger individuals won significantly more often in all species.

| | | Winner | | χ^2 | P | n |
		large	small			
N. vespilloides	males	63	14	29.92	0.001	77
	females	42	25	3.82	0.06	67
N. investigator	males	25	5	12.03	0.001	30
	females	18	7	4.00	0.05	25
N. vespillo	males	38	7	20.00	0.001	45
	females	19	8	3.70	0.10	27

Table 4. Test on the importance of early arrival in conflicts in *Nicrophorus*. The table shows which of the four possible individuals were found at the carcass at the end of the experiment. The result is different between species ($\chi^2=3.92$, $df=1$, $P<0.05$; two first and two last groups were pooled because of the small sample size): The symbols used are: m=males, f=females, e=early and l=late. For example, $m_e f_e$ means the first pair at the carcass.

| | Pair found at the carcass | | | | | | |
	$m_e f_e$	$m_e f_l$	$m_l f_e$	$m_l f_l$	χ^2	df	P
N. vespilloides	18	2	6	2	24.57	3	0.001
N. investigator	10	11	12	11	0.18	3	NS

3.3. Intraspecific conflicts

To study the importance of size in intraspecific conflicts two males and females of different size (size difference more than 15%) were released near the carcass simultaneously. The results of the experiment are shown in Table 3. In males the importance of size is very evident in all species and the larger individual was found at the carcass significantly more often than the smaller one. In females the trend is the same, but weaker (in males $P<0.001$ in all species, whereas in females the result is statistically significant in only one species). The lower number of cases in Table 3 for females in all species is due to their lower activity in the experiments.

The advantage of large size is also shown in this study by the field data, where pairs were collected at carcasses (see Fig. 1). In *N. vespilloides* both males and females found in these pairs are significantly larger than the mean sized individuals of the same species and the comparison of either fresh weight or elytra length gives a similar result (comparing elytra length: males in 14 out of 17 cases, binomial test, $P<0.01$, and females in 17 out of 20 cases, $P<0.01$, at three carcasses there were two females present and both are included). In *N. vespillo* only females are significantly larger than average (males in 4 out of 10 cases, NS, and females in 9 out of 11 cases, $P<0.05$, at one carcass there were two females). Unfortunately, there is no data on *N. investigator* pairs in nature.

The importance of arrival time was tested in *N. vespilloides* and *N. investigator* (Table 4). In this experiment, the two males and the two females released in the container were of equal size. The first pair was released near the carcass 4–5 hours before the second pair. The results of the two species tested differ from each other ($\chi^2=3.92$, $df=1$, $P<0.05$, the first and the

second, and the third and the fourth groups in Table 4 were pooled because of the small sample size). In *N. investigator* early arrival did not play any part at all and the final pair at the carcass was equally often any of the four possible combinations. In *N. vespilloides* the pair first released the carcass was found there together at the end of the experiment significantly more often than any other combination.

3.4. Interspecific conflicts

In experiments on interspecific conflicts females often seemed to avoid fighting with males of a different species, whereas males usually chased and bit these females. Although the results of intersexual fights in Table 5 are given separately for males and females, it is very likely that the results in females reflect the results in males. Therefore fights between males are considered to be more important.

In interspecific conflicts *N. vespilloides*, the smallest species, tended to lose to the other species. In conflicts between individuals of equal size (size difference 10% or less) *N. investigator* beat *N. vespilloides* in over two thirds of the cases and the difference is statistically significant (Table 5, the results are given separately for males and females). Another uneven pair of species was *N. vespilloides* and *N. vespillo*. In conflicts between individuals of equal size *N. vespillo* won significantly more often and there was a suggestion that *N. vespilloides* lost to *N. vespillo* even when it was larger (Fisher's exact test, $P<0.085$). Conflicts between equally sized individuals in *N. investigator* and *N. vespillo* were even.

In interspecific conflicts the reproductive state of females could be important. For example, individuals in species where females are not mature might fight

Table 5. Interspecific conflicts in *Nicrophorus*. The first column gives the number of conflicts which the species won even though the individual of this species was smaller than the opponent (the total number of conflicts where the individual of this species was smaller than the opponent is given in parentheses). χ^2-test results refer to the difference between the observed and expected (equal) probability of winning when the opponents are of equal size (second column).

Fighting species	Winner when smaller		same size	χ^2	P
Males:					
N. vespilloides / investigator	0	(4)	14		
	2	(9)	33	7.68	0.01
N. vespilloides / vespillo	0	(3)	3		
	14	(23)	18	9.33	0.01
N. investigator / vespillo	5	(10)	7		
	0	(2)	8	0.07	NS
Females:					
N. vespilloides / investigator	1	(3)	14		
	3	(10)	33	7.68	0.01
N. vespilloides / vespillo	0	(6)	4		
	13	(21)	15	6.37	0.05
N. investigator / vespillo	3	(5)	8		
	2	(3)	10	0.11	NS

less eagerly than their opponents. Fig. 3 shows the period when different *Nicrophorus* species are known to reproduce (the data is from my rearing experiments, see below) and the period when the interspecific experiments were conducted. Unfortunately, the rearing experiments were not designed to cover the whole reproductive period of the beetles and therefore, the real period could be even longer. However, this data should be important only for species that lose conflicts.

Fig. 3 shows that almost all experiments on *N. vespilloides* were conducted during the time when the females of this species were laying eggs in the rearing experiments and therefore, the reproductive state of females cannot explain its low success rate.

3.5. Intersexual interactions

How are breeding pairs at the carcasses formed? Do individuals of the same sex simply fight with each other, with the winner staying at the carcass, or could mate choice be involved? In the following experiment, the possibility that individuals choose their mates on the basis of their size, was studied. In the experiment a pair was allowed to stay together at a carcass for 3 to 4 hours and then the male and the
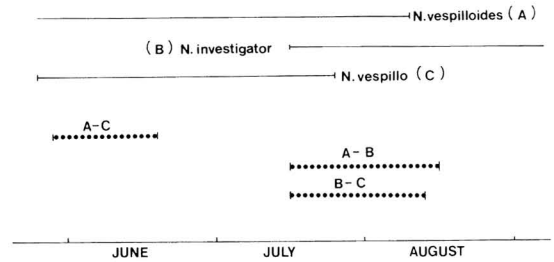

Fig. 3. Reproductive periods of the three *Nicrophorus* species and the timing of interspecific experiments. The reproductive period is the time when the females of different species were observed to lay eggs in the laboratory. Solid lines give the oviposition period of females and the dotted lines the timing of interspecific experiments. A = *N. vespilloides*, B = *N. investigator* and C = *N. vespillo*. See Material and methods for further explanation.

female were separated. Two new potential mates, one larger and one smaller than the original one, were then introduced separately to the remaining individual.

In most experiments both new mates were either accepted or rejected irrespective of their size, and no mate choice based on size took place (Table 6). There was no difference between males and females in this respect (χ^2=1.64, NS, pooled data from all species). Individuals showed rejection by intermittent biting and by pushing and chasing a new mate away (this was common behaviour in males), or by leaving the carcass (only females left the carcass). Very often, before chasing a new mate away males first copulated with her. On the other hand, when a new mate was accepted, the pair stridulated together and copulated almost immediately. After removing the new mates, the old mate was released and was accepted in all cases.

The new mates were frequently rejected (Table 6). In particular, *N. investigator* rejected most of the new mates, in 67.7% of the cases. On the contrary, the rejecting percentage is very low in *N. vespilloides*, only 23% (data on males and females combined). The difference between *N. investigator* and *N. vespilloides* is significant (χ^2=12.54, df=2, P<0.01; because of the small sample size the cases with one new mate accepted were pooled in Table 6). *N. vespillo* was intermediate and rejected a new mate in 43.6% of the cases, which is not significantly different from either of the other species (*N. vespillo* and *N. investigator*: χ^2=4.24, df=2, NS and *N. vespillo* and *N. vespilloides*: χ^2=3.65, df=2, NS). Therefore,

Table 6. Acceptance of a new mate in *Nicrophorus*. In the experiment, after separating a pair from each other, two new mates (one at a time) were introduced to the remaining individual at the carcass. There is no difference between males and females in their response (χ^2=7.395, df=6, NS; each species was first tested separately by using Fisher's exact test on two groups: 1) accepted at least one new mate and 2) did not accept either of the new mates, and then the probabilities were combined with Fisher's method). In a comparison between species, *N. investigator* and *N. vespilloides* differ from each other significantly (χ^2=12.54, df=2, P<0.01; males and females pooled) but the two other comparisons between the species are not significant (*N. investigator* vs *N. vespillo*: χ^2=4.24 and *N. vespilloides* vs *N. vespillo*: χ^2=3.65, both NS). See text for further explanation.

| | | Acceptance of a new mate | | | |
		Both	Smaller	Larger	Neither	n
N. vespilloides	males	7	2	0	3	12
	females	9	2	0	3	14
N. investigator	males	4	1	1	11	17
	females	2	2	0	10	14
N. vespillo	males	4	2	3	7	16
	females	11	0	2	10	23
Males		15	5	4	21	45
Females		22	4	2	23	51

although the experiment gave no evidence of mate choice based on size, it showed that the pair, while burying the carcass, learned to recognize each other.

3.6. Rearing experiments

Rearing experiments were conducted to see how the size of the carcass or the size of the female affect clutch size or larval size. It was difficult to get females to lay eggs in the containers and, in particular, *N. vespillo* was observed not to lay eggs on carcasses of 3.5 g. The multiple regression of clutch size and larval size in Table 7 has been calculated only for *N. vespilloides* because of the small sample size in the other species.

Table 7 shows that the number of larvae correlates significantly only with the size of the carrion and that female size is not significant. Larval size does not correlate with either of the independent variables.

If the size of the carcass is kept constant, the number of larvae is highest in *N. vespilloides* (Table

Table 7. Regression analysis on the effect of female size and carrion size on the number of last instar larvae and the weight of individual pupae in *N. vespilloides*. When obtaining the *t*-values the effect of the other independent variable was controlled. ***P<0.001.

	Carrion size	Female size	df
Number of larvae	10.69***	1.64	1,43
Weight of pupae	1.59	0.94	1,31

Table 8. The number of larvae produced in carcasses of different size in three species of *Nicrophorus* (mean ± *SD*). The number of rearing experiments is given in parentheses.

Carrion size (g)	*N. vespilloides*	*N. investigator*	*N. vespillo*
3.5	5.8 ± 2.6 (12)	3.0 ± 0.8 (4)	–
5.0	10.3 ± 2.5 (11)	5.3 ± 4.2 (6)	5 (1)
10.0	16.2 ± 5.9 (15)	6.8 ± 1.8 (13)	6.2 ± 2.6 (6)
20.0	26.6 ± 5.4 (8)	12.3 ± 4.7 (8)	7.5 ± 3.5 (2)

8). For example, with a carcass size of 10 g, *N.vespilloides* produces more than two times as many offspring as the two other species. Wilson & Fudge (1984) have shown that the same occurs in several North American species and, furthermore, Bartlett (1987) shows that the result is due to parents controlling the brood size by cannibalizing the larvae.

4. Discussion

The laboratory experiments in *Nicrophorus* showed that intraspecific conflicts are in most cases settled by the size difference between individuals. This is a well-known result in many species (see Introduction). In addition, the importance of size in nature was shown by the field data where individuals found in pairs at carcasses were larger than an average individual in the population. Moreover, in field experiments on North American species Wilson & Fudge (1984) found that the central male at the carcass was larger than the males at the periphery and they suggested that this resulted from intraspecific competition. All this data show that asymmetry in size is very important in conflicts in *Nicrophorus*.

Carrion is a highly temporary resource and individuals, independent of their size, arrive at it at dif-

ferent times. To arrive later might be disadvantageous, for example, individuals arriving first will have an opportunity to assess the value of the resource as well as to get information on the environment around the resource. This could create a payoff asymmetry between individuals and benefit the early arrivals. To remove the influence of size, the experiments were carried out with individuals of equal size. According to the results, arrival time was important only in one of the two species studied. In *N. vespilloides* the first pair was found at the carcass significantly more often than the individuals released later on. In the other species, *N. investigator,* arrival time did not have any observable effect.

Studies on interspecific competition have shown that larger species are more likely to be superior in competition (Schoener 1983). In *Nicrophorus* this was shown in the field by Easton (1979) and, according to him, *N. investigator* effectively stops the reproductive period of *N. vespilloides*. Is size, however, equally important in both intra- and interspecific conflicts? This question is important because of the large size variation within species where the smallest individual of the largest species can be clearly smaller that the largest individual of the smallest species.

The experiments on interspecific conflicts showed that in *N. vespilloides*, which was the smallest species in this study, individuals lost the carcass to the other species when smaller or even when of the same size. The other two species, when fighting against each other, were equal. This result suggests that species identity was used as an asymmetry in interspecific fights. In analysing animal conflicts Hammerstein (1981) showed that below some critical value of difference in fighting ability, individuals would respect a payoff-irrelevant asymmetry such as ownership. Besides ownership, species identity could be a good example of this kind of payoff-irrelevant asymmetry. However, a payoff-irrelevant asymmetry can be important only in cases where the cost of possible escalation is considerable when compared to the value of winning (Hammerstein 1981), as it may be in fights between *Nicrophorus* (Pukowski 1933). When studying fighting behaviour in three ant species, Jutsum (1980) found a similar kind of situation. According to his results, there was a clear hierarchy between the ant species and an individual belonging to an inferior species managed to win only when considerable larger than its opponent. In *N. vespilloides* the result on interspecific conflicts, as well the importance of arrival time in intraspecific conflicts, indicates that the species may be less competitive than the other species. This is particularly interesting because in a resource defence system small individuals could be expected to fight harder for a particular resource. This is because their likelihood of gaining access to another resource is much smaller than in large individuals and therefore, the value of the current resource is much higher (see Grafen 1987). However, this prediction relies on the rareness of empty resource patches and due to the differences in habitat and seasonal occurrence between the species *N. vespilloides* is likely to find carcasses with mainly intraspecific rivals at it.

Bartlett (1987) has shown that *Nicrophorus* parents can control the number of offspring produced at a particular carcass by killing their own offspring. This phenomenon is likely to explain the results in rearing experiments in this study where the number of larvae at a carcass depended on the size of the carcass and not on the size of the female. Cannibalism may allow the parents to 'decide' the number and hence the size of their offspring. In this study, *N. investigator* and *N. vespillo* produced markedly fewer offspring than *N. vespilloides* with the same amount of larval food, suggesting a different trade-off between the size and number of offspring in the three species. However, according to the field data, all the species studied had a very similar minimum size showing that even the large species have retained their ability to survive with only a small amount of larval food, a feature advantageous for species living in an environment where competition for food is strong (Putman 1983 and references therein).

In *Nicrophorus* both males and females fight and this is one probable reason why *Nicrophorus* beetles do not have any clear size difference in favour of males (in two of the species females were even larger than males). In many other fighting insect species where only males fight, males are larger than females or possess special weapons (e.g. Palmer 1978, Eberhard 1979, Hamilton 1979, Brown et al. 1985). The importance of intrasexual fights over carcasses was also confirmed by the experiments on mate choice which did not indicate any preference towards a larger mate either in males or females. The result supports the earlier conclusion that the large individuals breeding at carcasses are selected during intrasexual fights. The experiment also revealed that the male and female at a carcass may recognize each other and this mate recognition allowed them to behave aggressively towards intruders irrespective of their sex. When the original mate was released at the end of the experiment he or she was always accepted.

Wilson & Knollenberg (1984) suggest that in *Nicrophorus,* the final development of ovaries in females takes place only after they have found a carcass. In this way, the female which has stayed at the carcass for some hours could be more valuable to the male than a female who has just arrived, and male aggressiveness towards arriving females would be understandable. Also, my rearing experiments show that the only important variable determining the number of larvae at a carcass is the size of the carcass and that female size is not significant. In this respect, males do not benefit from having a large mate. On the other hand, it is difficult to see why females should reject new males. However, arriving males are likely to fight with the owner male and this could be disadvantageous for the female. This is supported by the fact that females frequently left the carcass when males started to fight (pers. obs.).

Could individual recognition be important in resource defence, the pair at the carcass defending it together? This question is interesting in both intra- and interspecific context but more data is needed. For example, one would have to know how soon individuals learn to recognize each other and how strong the pair bond is. Pair bonding may not be possible until there are only two individuals left at the carcass. If pair bonding is of any significance in defence it would work against species where the bond is weak, such as *N. vespilloides.* But it would also work against rare species, where the likelihood of finding a mate at one particular carcass is low. Pukowski (1933) reports that in her experiments males were not willing to bury the carcass in the absence of a female. In my experiments I noticed that males were not willing to fight for the carcass if no females were present. Therefore, a male or a female, without a mate and fighting against a pair, may lose the carcass.

In spite of its inferiority in interspecific conflicts *N. vespilloides* was the most abundant species in my data and it is the most abundant species in Pukowski's (1933) data, although her data does not cover the whole flying season of the species. In my data, *N. vespilloides* was less likely than the other species to be involved in interspecific conflicts. This is partly because of its abundance and partly because of its different niche requirements. In a patchy environment, characteristics such as the ability to quickly find the resource patches and produce many offspring are often favoured (Horn & MacArthur 1972, Putman 1983 discusses the life history strategies of *Nicrophorus*). There is no accurate data on how soon different species of *Nicrophorus* arrive at carcasses, but the results of Chapman & Sankey (1955) suggest that *N. vespilloides* could arrive at fresher carcasses than another larger English species, *N. humator.* Interestingly, and surprisingly, in North America, where most of the *Nicrophorus* species are different to those in Europe, *N. vespilloides* is a rare species and specializes in marsh habitats, probably due to interspecific competition (Wilson et al. 1984).

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