Original Article

What's love got to do with it? Ontogenetic changes in drivers of dispersal in a marine ectoparasite

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Sex-biased dispersal is common in nature and can influence the way in which organisms are distributed throughout the environment with consequences at the individual, population, community, and species level. Much of our understanding of what drives sex-biased dispersal stems from work on birds and mammals where dispersal tends to be female and male biased, respectively. Here, we draw on this large body of empirical and theoretical work on vertebrates to investigate what drives breeding dispersal in an ectoparasite, the salmon louse, *Lepeophtheirus salmonis*. We manipulated the density, sex, and developmental stage of lice on pairs of juvenile pink salmon (*Oncorhynchus gorbuscha*) hosts and show that the probability of leaving a host is density dependent at the preadult I stage and dependent on the presence of the opposite sex at preadult II and adult stages. Experiments in which louse movement was observed in groups of 25 individually infected hosts supported findings from individual experiments. Lice appeared to account for predation risk as they were 3 times more likely to disperse in the dark, when susceptibility to predation was low, than in the light. Our results support the hypothesis that asymmetry in reproductive investment shapes patterns of sex-biased dispersal and highlight the potential for drivers of dispersal to change with ontogeny. These findings are the first to establish what drives dispersal in the ecologically and economically important salmon louse and highlight the generality of the role mate competition plays in driving sex-biased dispersal across the animal kingdom. *Key words:* dispersal, parasite, sea lice, sex bias. *[Behav Ecol 22:588–593 (2011)]*

INTRODUCTION

Dispersal, the permanent movement of organisms from one habitat to another, is a fundamental life history response to spatio-temporal environmental variation (Clobert et al. 2001). Dispersal strategies evolve under selective pressures that both favor dispersal and select against it. Evolutionary stable patterns of dispersal are predicted to result from a balance between these forces. As selective pressures are often sex-specific, dispersal strategies can differ between the sexes, and indeed sex-biased dispersal is common in nature (Clobert et al. 2001). This has led to a large body of theoretical and empirical work aimed at understanding the proximate and ultimate drivers of sex-biased dispersal and their consequences at the individual, population, and species level.

Advances in our understanding of what drives and maintains sex-biased dispersal have largely stemmed from contrasting patterns of dispersal in mammals and birds where a number of hypotheses have been developed to explain patterns of sex-biased dispersal including inbreeding avoidance (Perrin and Mazalov 2000), resource competition (Greenwood 1980), and local mate competition (Perrin and Mazalov 2000). The direction of bias is predicted to depend on mating system; all 3 hypotheses predict male-biased dispersal in polygynous systems, whereas in monogamous systems, only the resource competition hypothesis predicts female-biased dispersal. Although the vast majority of empirical and theoretical

work has focused on birds and mammals, sex-biased dispersal has more recently been demonstrated in a handful of other taxa including fish (Hutchings and Gerber 2002; Croft et al. 2003), lizards(Olsson and Shine 2003), and invertebrates (Sundstrom et al. 2003; Beirinckx et al. 2006; Stevens et al. 2006; Bandilla et al. 2008). The majority of these studies involved detecting patterns of dispersal in the field with species that are polygynous and support the local mate competition hypothesis. However, there remains a paucity of controlled experimental investigation into what drives and maintains sex-biased dispersal outside of vertebrate taxa.

Practically absent from studies of sex-biased dispersal are parasites (but see Bandilla et al. 2008). Yet, parasites that can be facultatively transmitted, that is, can decide to leave a host after having been obligately transmitted earlier in their life cycle, offer a number of distinct advantages over free-living organisms in the study of dispersal: They are often short lived and occupy discrete habitats that are easily identified, replicated, and amenable to experimental manipulation. One such parasite is the salmon louse, *Lepeophtheirus salmonis*, a directly transmitted ectoparasite that is ubiquitous on farmed and wild salmon in the northern hemisphere. Its life cycle is characterized by 2 free-living naupliar stages followed by an infective copepodid stage, which seeks out and attaches to a host fish. This is followed by 4 chalimus stages, which are physically tethered to the surface of the host, and then 2 preadult and 1 adult stage, which are collectively known as motile stages, because they can move between hosts (Johnson and Albright 1991). Facultative adult male–biased movement among hosts, analogous to breeding dispersal in free-living organisms, has been observed under experimental conditions (Hull et al. 1998; Connors, Krkosek, et al. 2008), on salmon

farms (Ritchie 1997) and in the wild (Krkosek et al. 2007; Gottesfeld et al. 2009; Connors et al. 2010), however little is known about the underlying drivers of dispersal in motile lice.

Sea lice cost the global aquaculture industry in excess of 400 million USD annually (Costello 2009). Motile louse stages are the most pathogenic to hosts (Bjorn and Finstad 1998), may act as vectors of viral and bacterial pathogens (Nylund et al. 1991, 1994; Barker et al. 2009), and their ability to move among hosts may play an important role in the transmission of lice from farmed to wild salmon (Connors, Juarez-Colunga, et al. 2008; Connors et al. 2010). Thus, the movement of motile lice among hosts may have important economic and ecological consequences. Here, we empirically examine the relative importance of resources and access to mates in driving dispersal of motile stage *L. salmonis*, quantify a cost of moving among hosts, and provide insight into ontogenic changes in drivers of sex-biased dispersal.

METHODS

Collection and maintenance

Wild juvenile pink salmon (*Oncorhynchus gorbuscha*) were collected, examined for *L. salmonis* as described by Krkosek et al. (2005), and sorted based on infection. Fish (Mean ± standard deviation; fork length: 68 ± 4 mm; girth: 11 ± 2 mm) were then held for a minimum of 24 h in a partitioned $2 \times 0.5 \times 0.5$ m flow through trough and fed ad libidum twice daily. Experimental aquaria (see below) were held in flow through baths with water in each aquarium being 2/3 replaced every 24 h enabling temperature, salinity, and dissolved oxygen to be maintained between 10–15 °C, 29–32 and 8–10 mg/l, respectively (Connors, Juarez-Colunga, et al. 2008). Lice were removed from host fish as needed by transferring an infected host to a transparent bag with a small amount of seawater and then gently running ones fingers along the side of the host until the louse became dislodged.

Individual movement experiments

To test for an influence of access to mates and resources (i.e., density of conspecifics) on the propensity of lice to leave a host, we established pairs of uninfected size matched (fork length and girth) pink salmon fry, which were fin clipped (tip of right or left pectoral fin), and placed in 10-l aquaria. After a 24 h recovery period, 1 fish was randomly chosen to be artificially infected by placing motile lice in 250 ml of seawater with the fish to be infected until the desired number, stage, and sex of lice had attached (see experimental conditions below), whereas the other host was sham infected (i.e., placed in 250 ml of seawater for the same period of time as the to-be-infected fish).

Experimental conditions consisted of either a single louse sex or males and females together on a single host under 2 densities (2 or 4 lice host^{-1}/ca. 0.66 or 1.33 lice gram^{-1}) across the 3 motile stages, replicated a minimum of 10 times for each condition (Table 1). For adult females, only virgins were used, as verified by the absence of paired spermatophores (Ritchie et al. 1996). Trials were carried out under a12:12 photoperiod with roughly half of all trials beginning during the 12-h dark period and half starting during the 12-h light period, allowing us to test for an influence of illumination on movement among hosts. Twice daily (~07:00 and ~19:00) for 7 days, tanks were removed from their water bath, and the distribution of lice on hosts was recorded. At the end of each trial, lice were removed, and fish were released at their site of capture.

We analyzed the resulting dataset using generalized linear mixed effects models (GLMM) with binomial error (Pinheiro

Table 1

The number of trials (*n*) for each experimental combination of sea louse developmental stage, sex (single sex or both sexes), and density (number of lice host^{-1}, low: 2, high: 4) in individual movement experiments

Stage	Sex	Density	*n*
Preadult I	Male	Low	10
Preadult I	Male	High	11
Preadult I	Female	Low	12
Preadult I	Female	High	11
Preadult I	Male/female	Low	12
Preadult I	Male/female	High	10
Preadult II	Male	Low	11
Preadult II	Male	High	11
Preadult II	Female	Low	10
Preadult II	Female	High	10
Preadult II	Male/female	Low	14
Preadult II	Male/female	High	12
Adult	Male	Low	10
Adult	Male	High	10
Adult	Female	Low	10
Adult	Female	High	12
Adult	Male/female	Low	11
Adult	Male/female	High	11

and Bates 2000). This allowed us to account for the fact that there was more than 1 louse observation per fish while testing for an influence of louse density, sex, and presence of the opposite sex on the probability of leaving a host. Analysis began with the building of a maximal model with density, sex, presence of the opposite sex, and all interactions as independent variables using maximum likelihood estimation. We then sequentially removed model terms testing their significance using likelihood ratio tests (Hilborn and Mangel 1997) until a minimum adequate model remained. We predicted that dispersal would be positively density dependent if it were driven by competition for resources, negatively density dependent if it were driven by the need to overcome host defenses, and dependent on the presence of the opposite sex if it were driven by access to mates.

Group movement experiments

Although the preceding experiments allowed for detailed replicated manipulations of fish and lice, juvenile salmonids are normally found in schools of tens to thousands (Groot and Margolis 1991). In order to more closely approximate natural conditions, we therefore conducted a series of experiments that examined movement among hosts in larger groups. Wild-caught juvenile pink salmon were examined for motile stage lice in transparent seawater filled bags and placed in 77-l aquaria until there were 25 fish with a single motile louse on each host and roughly equal numbers of each louse sex in each aquaria (Table 2). This was replicated 12 times with each trial running for 96 h at which point fish were removed and the distribution, sex, and stage of lice noted. We determined if the distribution of motile lice at the end of the trials was aggregated and, if so, tested whether there were significantly more male–female pairings than expected based on chance alone using a chi-square test. We predicted that if dispersal were driven by competition for resources, lice would remain evenly distributed among hosts at the end of the trials; if dispersal were driven by the need to overcome host defenses, lice would be aggregated on hosts at the end of the trials; and if dispersal were driven by access to mates, aggregation would result in more male–female pairs than expected based on chance alone. Furthermore, we predicted that if these drivers change with

Table 2
Summary of group experiments

Trial	Preadult I	Preadult II	Adult	Male	Female	Total lice	Opposite-sex pairs	Same-sex pairs
1	19	5	1	14	11	25	2	4
2	19	5	1	14	11	25	1	1
3	17	8	0	17	8	25	2	1
4	14	3	8	11	14	25	2	1
5	23	2	0	14	11	25	1	2
6	9	13	3	14	11	25	2	2
7	5	17	3	13	12	25	3	1
8	0	12	13	15	10	25	4	1
9	0	15	15	14	11	25	4	2
10	7	16	2	11	14	25	4	2
11	0	0	25	12	13	25	6	1
12	0	1	24	12	13	25	4	1

Number of preadult and adult lice at the beginning of each trial (1 louse per fish) and the number of opposite-sex and same-sex pairs observed on hosts at the end of each trial.

ontogeny, they should be reflected by changes in these patterns as the proportion of lice in each trial shifted from being dominated by preadult I lice to preadult II and then adult lice.

Predation experiments

The movement of parasites from one host to another is a risky endeavor. One such risk is predation from other organisms including their hosts; motile stage sea lice are of the same size class (Johnson and Albright 1991) as juvenile pink salmon's primary prey (zooplankton; Groot and Margolis 1991), and motile lice are occasionally seen being consumed by juvenile salmon (Connors BM, Lagasse C, personal observation). In light of the potential for hosts to act as predators, we sought to examine the relative susceptibility of each motile stage and sex to predation by juvenile pink salmon.

Uninfected juvenile pink salmon were assigned to 8-l aquaria with a single motile louse added 2 h later. Half of the trials began under a 12-h light cycle with the other half under a 12-h dark cycle. Every 12 h, tanks were observed to determine if the louse had attached to the fish or been consumed, with observations and switching of the light regime continuing every 12 h until attachment or consumption occurred. Fish were not fed during the course of this experiment, and trials were replicated 9–13 times per stage, sex, and light regime (Table 3).

Dissection to examine stomach contents confirmed consumption of lice by juvenile salmon in the first 10 trials where lice disappeared. In each of these 10 trials, a single louse was found, confirming consumption by the pink salmon. In the remaining trials, consumption was verified by examination of salmon feces for an undigested louse carapace, which was conspicuous compared with the rest of the faecal contents. There were 4 trials in which louse consumption could not be confirmed, and these trials were excluded from subsequent analysis. The proportion of lice that were consumed by hosts was compared among sexes, stages, and light regimes using chi-squared tests with Yates' correction for continuity when expected counts were less than 5. We predicted that if susceptibility to predation were a function of conspicuousness, lice would be more likely to be consumed during light periods and at larger sizes (i.e., developmental stages).

RESULTS

Individual movement experiments

In 4 of 12 high-density (4 lice host^{-1}) adult female trials, the infected fish died, and so these trials were excluded from the analysis. Louse movement was positively density dependent for preadult I lice (GLMM density term:$\chi^2 = 4.23$, degrees of freedom [df] = 1, $P = 0.039$; Figure 1) and dependent on the presence of the opposite sex for preadult II males (GLMM sex x presence of opposite-sex interaction term:$\chi^2 = 5.68$, df = 1, $P = 0.017$; Figure 1) and adult males (GLMM sex x presence of opposite-sex interaction term: $\chi^2 = 3.98$, df = 1, $P = 0.046$; Figure 1). Lice were significantly more likely to leave a host during a dark period than a light period (light: 26 of 101 movement events; dark: 75 of 101 movement events; $X_1^2 = 23.78$, $P < 0.0001$).

Group movement experiments

At the end of each trial, lice were aggregated among hosts, and aggregations were roughly twice as likely to result in a male–female pairing than a same-sex pairing. ($X_1^2 = 4.74$, $P = 0.029$; Table 2). The degree of aggregation (proportion of hosts with >1 louse) was positively correlated with the proportion of preadult II and adult lice at the beginning of the trial ($R^2 = 0.36$, $P = 0.023$; Figure 2). The proportion of pairings that were opposite-sex pairings was also positively related to the proportion of lice in the trial that were preadult II and adult stages ($R^2 = 0.69$, P < 0.001; Figure 3).

Table 3
Summary of predation experiments

Sex/stage	Light				Dark		
	n	Eaten	Unattach	Attach	n	Eaten	Unattach
Preadult I male	10	4	1	1	11	0	0
Preadult I female	9	6	1	1	10	0	0
Preadult II male	10	4	2	2	11	0	0
Preadult II female	11	5	2	2	11	0	0
Adult male	10	2	1	0	10	0	0
Adult female	13	4	7	6	11	0	0
Total	63	25	14	12	64	0	0

Number of trials (n), number of lice consumed (eaten), and the number of lice that remained unattached or that successfully attached to hosts after 12 h of light or dark.
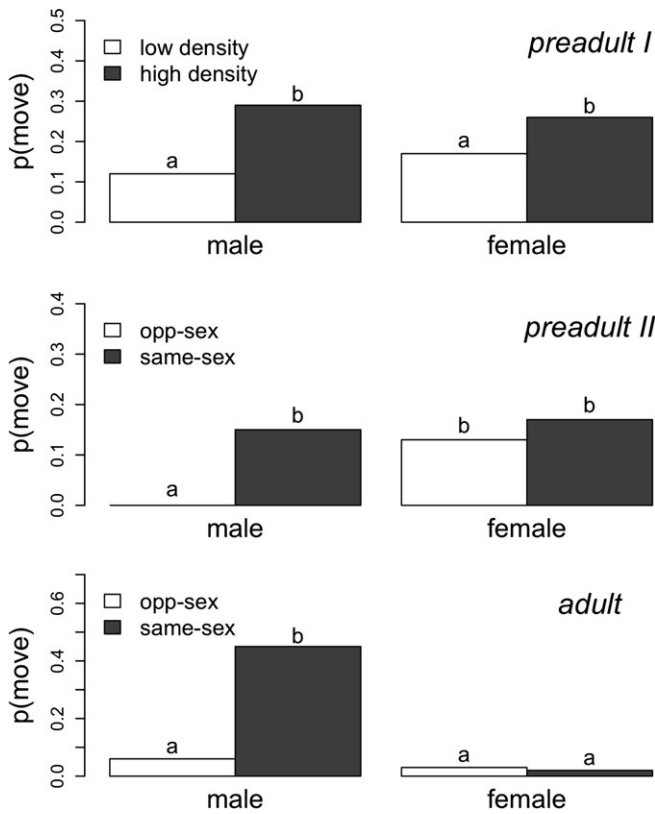
Predation experiments

Consumption of lice by pink salmon occurred in 25 of the 63 trials that began in the light and in none of the trials

Figure 1
When do lice leave a host? The probability preadult I, II, and adult lice leave a host as a function of sex and density (preadult I) and presence or absence of the opposite sex (preadult II, adults). Bars sharing lowercase letters are not significantly different (based on generalized linear mixed effects analysis).

that began in the dark ($X_1^2 = 67.17$, $P < 0.001$; Table 3). Excluding those trials where a louse was consumed, attachment occurred significantly more often in the first 12 h if the trial began in the dark (dark: 64/64; light 24/38; $X_1^2 = 27.67$, $P < 0.001$). Of the 14 trials that began in the light, and in which lice remained unattached and uneaten
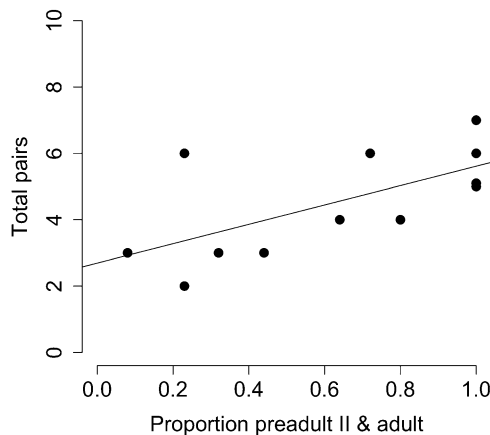
Figure 2
Relationship between the proportion of preadult II and adult lice in a group movement trial and the degree of aggregation (number of hosts with >1 louse) at the end of the trial ($y = 2.69 + 2.92x$, $R^2 = 0.36$, $P = 0.022$).
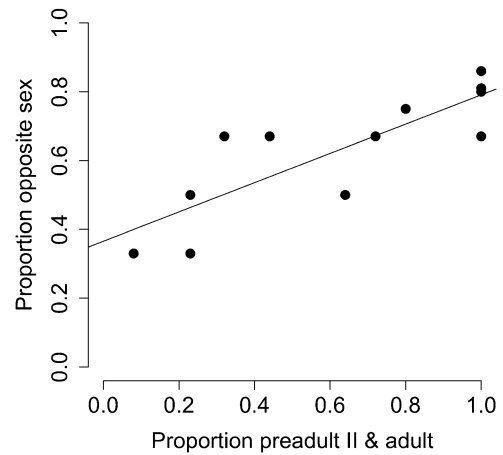

Figure 3
Relationship between the proportion of preadult II and adult lice in a group movement trial and the proportion of louse pairings on hosts at the end of the trial that were of opposite sex ($y = 0.37 + 0.43x$, $R^2 = 0.69$, $P < 0.001$).

after 12 h, lice were able to successfully attach to the host during the subsequent 12-h dark period in all but 2 cases. The likelihood of being consumed by a pink salmon host did not differ by louse sex or stage ($X_5^2 = 4.94$, $P = 0.462$).

DISCUSSION

We provide evidence to support the hypothesis that both competition for resources and access to mates influence dispersal and that the importance of these drivers shifts with ontogeny. In individual movement experiments, competition for resources drove dispersal at the preadult I stage, whereas competition for mates drove dispersal at the preadult II and adult stage. These drivers were not sex specific for preadult I lice but at the preadult II stage males were less likely than females to disperse when the opposite sex was present, and males were more likely than females to disperse in the absence of the opposite sex at the adult stage.

Sex-biased dispersal is predicted to arise when the benefit to cost ratio of dispersal differs between sexes. Predation did not differ by sea louse sex or stage, though susceptibility to predation was strongly influenced by light levels and motile lice appeared to take this into account as they were approximately 3 times more likely to move in the dark, when predation risk was lower, than during light periods. These findings suggest that predation risk is incorporated into sea louse dispersal decisions and that the costs of movement among hosts do not vary significantly between sexes or stages. Similar behavior is widespread in zooplankton, which undergo diurnal vertical migrations to avoid predation by fish (Lampert 1993), and has also been documented in some benthic invertebrates where males move into the water column in search of mates at night (Tully and Ceidigh 1987).

The absence of sex-specific costs of movement among hosts suggests that sex-biased patterns of dispersal in sea lice result from sex-specific benefits to movement. Sea lice are polygynous, and adult males provide no investment in offspring beyond sperm, whereas adult females invest both time and energy. Male fitness is therefore dependent on access to mates, whereas female fitness is contingent on access to resources for egg production. The resulting asymmetry in reproductive investment likely underlies sex-specific benefits of dispersal as lice approach sexual maturity. At the preadult

I stage, when lice are approximately 33% (females) to 50% (males) of their adult size (Johnson and Albright 1991), lice of both sexes should benefit by maximizing resources available for development to sexual maturity and so competition for host resources is an important driver of dispersal. Lice at the preadult II stage are closer to their adult size (females 60% of adult size, males 80%), and preadult II adult males can mate guard females until they are sexually mature. This suggests that at the preadult II stage, males should benefit to a greater extent than females by remaining on hosts with the opposite sex so as to ensure access to mates once they are sexually mature. Once lice are adults, males can mate repeatedly and so fitness is proportional to the total number of mates a male secures; females on the other hand only need to mate once (but see Todd et al. 2005) so fitness is proportional to investment in resource acquisition and the production of offspring. Adult males therefore benefit to a greater extent than adult females by dispersing from a host if there are no mates available. Group experiments, more closely mimicking natural conditions, confirmed the shift in drivers of dispersal observed in the individual trials. Lice were aggregated at the end of group trials, and there was a positive relationship between the proportion of lice in the trial that were preadult II and adults and both the degree of aggregation and the proportion of aggregation events with the opposite sex.

We assume that the juvenile pink salmon used in our experiments were homogenous in their suitability as hosts. This is likely an oversimplification as host compatibility, including immune response to infection and/or host behavior could influence movement of lice among hosts by creating heterogeneous host environments (Costello 2006). In an effort to control for the potentially confounding influence of host compatibility, we randomly selected uninfected hosts from the field for our experiments, nonetheless the influence of host compatibility on louse dispersal requires further research. We also assumed that louse densities were high enough to limit resources as has been suggested by observations of lice on farmed salmon (McKenzie et al. 2004). This appeared to be the case at the preadult I stage, and although resources did not influence dispersal decisions at the preadult II and adult stages, it is still likely that host resources were limiting as host mortality did occur in some high-density treatments, at least for adult females.

Sex-biased dispersal can have important consequences for disease transmission and dynamics (e.g., Robertson et al. 2006), and sea lice are no exception. Motile lice may act as vectors of viral and bacterial pathogens, which could contribute to pathogen transmission among and between farmed and wild hosts. Our findings are the first to identify when and why lice move among hosts and can advise the development of integrated pest management strategies on salmon farms, which account for louse behavior. In addition, an improved understanding of the drivers of louse dispersal may help to mitigate the impacts of louse transmission from farmed to wild salmon in areas of intensive salmon aquaculture and sympatric wild salmon populations.

FUNDING

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