Anywhere but here: local conditions alone drive dispersal in *Daphnia*

Philip Erm*, Matthew D. Hall†, and Ben L. Phillips‡

June, 2018

Abstract

Dispersal is fundamental to population dynamics and it is increasingly apparent that most organisms make dispersal decisions based upon information gathered from the environment. Ideally, organisms would make fully informed decisions, with knowledge of both intra-patch conditions (conditions in their current location) and extra-patch conditions (conditions in alternative locations). Acquiring information is costly, however, and extra-patch information will typically be costlier to obtain than intra-patch information. As a consequence, theory suggests that organisms will often make partially informed dispersal decisions, utilising intra-patch information only. We test this proposition in an experimental two-patch system using populations of the aquatic crustacean, *Daphnia carinata*. We manipulated conditions (food availability) in the population's home patch, and in its alternative patch. We found that *D. carinata* made use of intra-patch information (resource limitation in the home patch induced a ten-fold increase in dispersal probability) but made no use of extra-patch information (resource limitation in the alternative patch did not affect dispersal probability). Our work highlights both the very large influence that information can have on dispersal probability, but also that dispersal decisions will often be made in only a partially informed manner.

Keywords: resource-dependent dispersal, information use, *Daphnia carinata*, biological invasion

philip.erm@unimelb.edu.au, School of BioSciences, The University of Melbourne, Victoria, Australia
†*matthew.hall@monash.edu*, School of Biological Sciences, Monash University, Victoria, Australia
‡*phillipsb@unimelb.edu.au*, School of BioSciences, The University of Melbourne, Victoria, Australia

Introduction

It is increasingly appreciated that dispersal is, like survival and reproduction, a fundamental facet of life history (Bonte and Dahirel 2017). Dispersal behaviours can have profound consequences for individual fitness, and the variety of dispersal behaviours in a population not only influences local population dynamics, but also metapopulation and evolutionary dynamics across a species range (Clobert et al. 2001). For reasons of simplicity, the vast majority of ecological and evolutionary models that incorporate dispersal assume that the decision to disperse is uninformed; that individuals decide to move, or decide how far to move, in an information vacuum (*e.g.*, models utilising reaction-diffusion or integrodifference equations; Fisher 1937; Skellam 1951; Kot et al. 1996; but see Fronhofer et al. 2016). There is now considerable evidence, however, that dispersal decisions are typically informed by aspects of the environment (Clobert et al. 2009), and such information use can be expected to have non-negligible effects on ensuing population and evolutionary dynamics (Delgado et al. 2014; Ponchon et al. 2015; Urban et al. 2016).

The most common form of informed (or condition-dependent) dispersal is density-dependent dispersal (Bowler and Benton 2005). Here, individuals acquire information about population density, and, if conditions more favourable to survival and reproduction are likely to be found elsewhere, make the decision to disperse. When all else is equal, high density – with greater competition for resources, greater rates of disease transmission and so on – will be associated with poorer conditions (Bowler and Benton 2005). It has been repeatedly demonstrated that individuals acquire information on density and act upon it (*e.g.*, De Meester and Bonte 2010; Fellous et al. 2012; Martorell and Martínez-López 2014; Fronhofer et al. 2017a). In many species, this information is acquired through food limitation (Fronhofer et al. 2017b): when nutrition is limited, particularly in juvenile stages, individuals tend to be more dispersive. Information on the relative merits of different alternative locations can also be acquired in numerous ways, including prospecting (actively moving through, and assessing, new locations, *e.g.*, Pärt and Doligez 2003) and by observing immigrating conspecifics (*e.g.*, Cote and Clobert 2007).

Several evolutionary models have now been constructed to examine the evolution of informed dispersal (*e.g.*, Bocedi et al. 2012; Delgado et al. 2014), and while these models are in general agreement that informed dispersal will often evolve, much hinges on the ease with which information is acquired, and the value of that information (Poethke et al. 2016). The models raise intriguing questions about investment in information gathering: if an organism only assesses local, intra-patch, conditions, how can it be sure that another location is better? When should an individual invest in acquiring information beyond its home patch? Ideally, of course, individuals would have both intra- and extra-patch information to make an informed decision, but acquiring such information will almost always entail a cost (time, energy, survival; Bonte et al. 2012). Thus, it may often be the case that individuals act on the limited information that is most easily acquired: intra-patch information.

Here, we examine dispersal between patches in experimental populations of the aquatic crustacean, *Daphnia carinata*. In *Daphnia* generally, dispersal has been shown to promote population stability in pond metacommunities and fluctuating environments (Howeth and

Leibold 2010; Steiner et al. 2016), and has also been used to highlight colonisation processes after glaciation events (Weider and Hobæk 1997). Moreover, it may likewise have importance for informing the management of zooplankton invasions, such as that of the spread of *Daphnia lumholtzi* across North America (Dzialowski et al. 2000; Havel et al. 2002). Although dispersal in *Daphnia* is usually characterised as being driven by the passive transport of ephippia (long-lived resting eggs) by water fowl or other vectors (Allen 2007; Frisch et al. 2007; Van de Meutter et al. 2008), individuals can also actively disperse between permanently or temporarily interconnected water bodies (Michels et al. 2001; Cottenie et al. 2003). Since *Daphnia* have been shown to physiologically adapt aspects of their life history – such as reproduction, growth, and immune investment – to suit local conspecific population densities (Goser and Ratte 1994; Burns 2000; Lürling et al. 2003; Michel et al. 2016), it appears probable that they may likewise adjust their rates of active dispersal in response to local conditions. Although it has been demonstrated that *Daphnia* do increase ephippia production at high population densities (Carvalho and Hughes 1983; Hobaek Anders and Larsson Peter 1990), presumably boosting passive dispersal opportunities, the effects of information use, density, and resource limitation on their active dispersal have not been explored.

Using *D. carinata* then, we conduct a simple experiment to determine whether, like many other species, individual *D. carinata* respond to resource limitation by increasing their rates of active dispersal. We also ask whether this response is contingent upon extra-patch information; the presence or absence of ad libitum food in the neighbouring patch.

Methods

Laboratory population of *D. carinata*

All *D. carinata* used were genetically identical members of a single clone line. The founding member of this lineage was collected at 38°10'34.3"S, 144°21'14.1"E (a lake in Geelong, Victoria, Australia) in October 2016. Its offspring were used to establish laboratory stock cultures, which were housed in glass jars containing 300 ml of ADaM zooplankton medium and kept within growth chambers maintained at 22° C on a 12.30 light:11.30 dark photoperiod (Klüttgen et al. 1994; as modified by Ebert 2013). Stocks were fed the green algae *Scenedesmus*. In order to reduce any potential impact of maternal effects, all individuals used in the experiment were taken from stocks that were maintained under these conditions for at least two generations.

Experimental materials and conditions

We set up two-patch microcosms with which to measure dispersal of *Daphnia*. Each patch was a 950 ml plastic Cryovac XOP-0980 container filled with 600 ml of ADaM and kept on bench tops in an open air laboratory. The laboratory was maintained at 22° C and each container was covered with a transparent plastic sheet that was only removed during feeding

and data collection. From their base, each container's dimensions were 90 mm x 75 mm x 110 mm, and they possessed a gradual taper from top to bottom, such that the opening at the top of the container (100 mm x 90 mm) was larger than the base of the container. A circular hole with a diameter of 15 mm was centrally located 35 mm above the base on one of the long sides of each container. This was connected to plastic PVC piping of an identical internal diameter that linked one container to the next, acting as a tunnel through which *D. carinata* could disperse between the two patches. At the commencement of the experimental trials, dispersal between containers was prevented by inserting cotton balls into the openings of the connecting tunnel.

Food availability experiment

Within this two-patch system, we examined the effect of intra- and extra-patch food availability on the dispersal rate of *D. carinata*. We seeded one half of each two-patch system with 10 adult females taken from stock cultures, and allowed this population to grow for 9 days in the experimental system while dispersal was blocked. This resulted in an average of 122 individuals across a variety of age and size classes in each population. On the 10th day we then opened the dispersal tunnels and 96 hours later censused the population in both patches to determine the number of individuals that had dispersed into the newly available patch. As individuals born during the dispersal period could not be distinguished from those present at its beginning, all individuals in the final census were treated as though they had been present in patch 1 at the start of the 96 hours.

Our patch pairs were allocated to four treatment combinations (n = 5 per combination) according to a two factor crossed design in which we independently modified food availability in the two patches. Factor 1 was intra-patch food availability: once the dispersal tunnel was opened, half of the populations no longer received food in their starting patch. Factor 2 was extra-patch food availability: here we either daily added food to the second patch (commencing three days before dispersal was allowed) or withheld food from this patch. This meant that half of the populations were dispersing into patches containing no food at all, and the other half into patches with an abundance of food. Food in this case was a daily fed mixture of 8 million *Scenedesmus* sp. cells (an unidentified Australian *Scenedesmus*) and 12 million *Scendesmus obliquus* cells.

The probability of individuals dispersing was compared between treatment combinations using a generalised linear model with binomial errors and a logit link, with each individual in each population being characterised as a trial in which either success (dispersing into patch 2) or failure (remaining in patch 1) resulted. All statistical tests were performed in R version 3.4.1 (R Core Team 2016).

Results

There was no significant interaction between intra- and extra-patch feeding treatments ($z = 1.07$, $P = 0.283$; Table 1), and likewise no significant effect of food availability in patch 2 ($z = 1.12$, $P = 0.262$; Table 1). There was, however, a significant effect of food availability in patch 1 ($z = 10.94$, $P < 0.001$; Table 1), with intra-patch food deprivation resulting in an approximately ten-fold higher probability of dispersing (food-deprived, mean = 0.259, SE = 0.026; normally-fed, mean = 0.022, SE = 0.005; Figure 1).

Discussion

The fitness benefit flowing to a dispersing individual depends on both the quality of the home patch, as well as the quality of the new patch. As a consequence, in an ideal world, we would expect dispersal decisions to be made on a balance of 'push' factors, such as local patch conditions, and 'pull' factors, such as the quality of other patches. The quality of the new patch should be high enough (relative to the home patch) that it offsets the fitness costs of moving. But organisms do not live in an ideal world: information can be costly to acquire, and there is a likely asymmetry of cost such that information about alternative patches is harder to obtain than information about an individual's home patch. Because of this, we might expect pull factors – requiring costly information gathering – to be less important in dispersal decisions than push factors. Our results support this expectation. In our system, there was a significant increase in inter-patch dispersal when *D. carinata* were deprived of food (Figure 1), so it is clear that *D. carinata* exploited intra-patch information to inform their dispersal decisions. By contrast, extra-patch conditions (food either abundant or entirely absent) had no effect on dispersal rates. Thus it also appears that *D. carinata* either did not use, or were incapable of using, extra-patch information to inform their dispersal decisions.

Our first result – that animals increase dispersal propensity under conditions of resource shortage – has been well established empirically. Studies on taxa ranging from plants to invertebrates and vertebrates either imply, or experimentally demonstrate, that resource shortage is a powerful piece of information motivating dispersal (*e.g.*, Bowler and Benton 2005; Martorell and Martínez-López 2014; Fronhofer et al. 2017b). Our study adds *Daphnia carinata* to the long list of organisms that exploit this piece of intra-patch information. It also demonstrates, however, that the effects of resource deprivation on dispersal may be extremely pronounced, with 25.9% of individuals dispersing when food deprived as opposed to only 2.2% of individuals when better fed (Figure 1). This suggests that ecological models may benefit substantially from accounting for factors like resource availability that can have a very large effect on dispersal behaviour.

Our second result – that the presence or absence of food in the second patch had no effect on dispersal – highlights the relative importance of push versus pull factors in driving a populations movement. In the present case, to obtain information that would draw *Daphnia* into the second patch, individuals either had to engage in prospecting within the inter-patch

tunnel and the second patch, or to sense extra-patch conditions remotely. We found no evidence to suggest that either source of information was exploited (Figure 1). In natural populations, extra-patch information gathering behaviours like prospecting are predicted to be costly due to the threat of predation that comes from moving into novel environments (Bonnet et al. 1999; Hiddink et al. 2002; Bonte et al. 2012), or the simple energetic cost of having to move to assess new patches (Delgado et al. 2014). Here, the dominance of resource limitation in pushing dispersal from the local patch indicates that the pull to move into new patches was relatively weak in comparison, either because obtaining more information was costly, or because that information was in some way imperceptible.

Although this finding supports the prediction that potentially expensive extra-patch information will not be sought out compared to relatively inexpensive intra-patch information, it remains possible that *D. carinata* would ordinarily exploit other forms of extra-patch information were it more readily available to them than in this experimental context. For instance, a lack of migrants moving back from patch 2 to patch 1 may have made it impossible for *D. carinata* to encounter migrating conspecifics, a relatively cheaply-acquired form of extra-patch information that has been shown to inform dispersal decisions in other taxa. In lizards, for example, residents may recognise immigrants and assess their condition and number to make inferences about extra-patch conditions (Cote and Clobert 2007). The same phenomenon has also been shown in simpler organisms, such as ciliates (Jacob et al. 2015). In our system however, individuals that reached patch 2 in treatments where it was well resourced, and so capable of producing migrants that could signal that fact, would have had no incentive to return to patch 1. Moreover, that the population size of patch 2 was invariably smaller than patch 1 meant that there would have been a lower absolute number of individuals capable of dispersing from there, regardless of conditions.

In conclusion, our results add to the growing body of evidence that condition-dependent dispersal is the norm amongst taxa, and that it is moreover capable of generating substantial differences in dispersal behaviour (*e.g.*, Legrand et al. 2015; Fronhofer et al. 2017b). This growing empirical consensus warns against the simplifying assumption – used in the majority of ecological and evolutionary models – that dispersal rate is constant with respect to conditions. Relaxing that assumption is now well justified on empirical grounds, and the magnitude of shift in dispersal resulting from condition dependence suggests that it will have non-trivial effects when incorporated into mechanistic models of evolution, population dynamics, invasion spread, and so on (*e.g.*, Armsworth 2008; Armsworth and Roughgarden 2008). In this light, the relative use of extra- vs intra-patch information is important because when we move to a conditional dispersal model, the obvious simplifying assumption is that organisms exploit only intra-patch information. Our results suggest that intra-patch information is dominant in *Daphnia carinata*, but the degree to which this is true generally will determine how complex our models of dispersal really need to be.

Acknowledgements

We thank Katrina-Lee Ware and Hannah Edwards for their invaluable assistance in the preparation of the experimental set-up. Funding was provided by the Australian Research Council (DP160101730; FT160100198).

References

Allen MR (2007) Measuring and modeling dispersal of adult zooplankton. Oecologia 153:135–143. doi: 10.1007/s00442-007-0704-4

Armsworth PR (2008) The evolution of non-random movement along clines. Evolutionary Ecology Research 10:967–985

Armsworth PR, Roughgarden JE (2008) The structure of clines with fitness-dependent dispersal. The American Naturalist 172:648–657. doi: 10.1086/591685

Bocedi G, Heinonen J, Travis JM (2012) Uncertainty and the role of information acquisition in the evolution of context-dependent emigration. The American Naturalist 179:606–620. doi: doi.org/10.1086/665004

Bonnet X, Naulleau G, Shine R (1999) The dangers of leaving home: Dispersal and mortality in snakes. Biological Conservation 89:39–50. doi: 10.1016/S0006-3207(98)00140-2

Bonte D, Dahirel M (2017) Dispersal: A central and independent trait in life history. Oikos 126:472–479. doi: 10.1101/065151

Bonte D, Van Dyck H, Bullock JM et al (2012) Costs of dispersal. Biological Reviews 87:290–312. doi: 10.1111/j.1469-185X.2011.00201.x

Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: Relating individual behaviour to spatial dynamics. Biological Reviews 80:205–225. doi: 10.1007/978-94-011-2338-9_3

Burns CW (2000) Crowding-induced changes in growth, reproduction and morphology of Daphnia. Freshwater Biology 43:19–29. doi: 10.1046/j.1365-2427.2000.00510.x

Carvalho GR, Hughes RN (1983) The effect of food availability, female culture-density and photoperiod on ephippia production in Daphnia magna Straus (Crustacea: Cladocera). Freshwater Biology 13:37–46. doi: 10.1111/j.1365-2427.1983.tb00655.x

Clobert J, Danchin E, Dhondt AA, Nichols J (2001) Dispersal. Oxford University Press, New York

Clobert J, Galliard L, Cote J et al (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology letters 12:197–209.

doi: 10.1111/j.1461-0248.2008.01267.x

Cote J, Clobert J (2007) Social information and emigration: Lessons from immigrants. Ecology letters 10:411–417. doi: 10.1111/j.1461-0248.2007.01032.x

Cottenie K, Michels E, Nuytten N, Meester LD (2003) Zooplankton Metacommunity Structure: Regional Vs. Local Processes in Highly Interconnected Ponds. Ecology 84:991–1000. doi: 10.1890/0012-9658(2003)084[0991:ZMSRVL]2.0.CO;2

De Meester N, Bonte D (2010) Information use and density-dependent emigration in an agrobiont spider. Behavioral Ecology 21:992–998. doi: 10.1093/beheco/arq088

Delgado MM, Bartoń KA, Bonte D, Travis JMJ (2014) Prospecting and dispersal: Their eco-evolutionary dynamics and implications for population patterns. Proceedings of the Royal Society of London B: Biological Sciences 281:20132851. doi: 10.1098/rspb.2013.2851

Dzialowski AR, O'Brien WJ, Swaffar SM (2000) Range expansion and potential dispersal mechanisms of the exotic cladoceran Daphnia lumholtzi. Journal of Plankton Research 22:2205–2223. doi: 10.1093/plankt/22.12.2205

Ebert D (2013) Artificial Daphnia medium: ADaM (Aachener Daphnien Medium). In: TheEbertGroup. http://evolution.unibas.ch/ebert/lab/adam.htm. Accessed 30 May 2018

Fellous S, Duncan A, Coulon A, Kaltz O (2012) Quorum sensing and density-dependent dispersal in an aquatic model system. PLoS One 7:e48436. doi: 10.1371/journal.pone.0048436

Fisher RA (1937) The wave of advance of advantageous genes. Annals of Eugenics 7:355–369. doi: 10.1111/j.1469-1809.1937.tb02153.x

Frisch D, Green AJ, Figuerola J (2007) High dispersal capacity of a broad spectrum of aquatic invertebrates via waterbirds. Aquatic Sciences 69:568–574. doi: 10.1007/s00027-007-0915-0

Fronhofer EA, Gut S, Altermatt F (2017a) Evolution of density-dependent movement during replicated experimental range expansions. bioRxiv. doi: 10.1101/114330

Fronhofer EA, Legrand D, Altermatt F et al (2017b) Bottom-up and top-down control of dispersal across major organismal groups: A coordinated distributed experiment. bioRxiv 213256. doi: 10.1101/213256

Fronhofer EA, Nitsche N, Altermatt F (2016) Information use shapes the dynamics of range expansions into environmental gradients. Global Ecology and Biogeography 26: doi: doi.org/10.1101/056002

Goser B, Ratte HT (1994) Experimental evidence of negative interference in Daphnia magna. Oecologia 98:354–361. doi: 10.1007/bf00324224

Havel JE, Shurin JB, Jones JR (2002) Estimating dispersal from patterns of spread: Spatial and local control of lake invasions. Ecology 83:3306–3318. doi: 10.2307/3072081

Hiddink J, Kock R, Wolff W (2002) Active pelagic migrations of the bivalve Macoma balthica are dangerous. Marine Biology 140:1149–1156. doi: 10.1007/s00227-002-0794-9

Hobaek Anders, Larsson Peter (1990) Sex Determination in Daphnia Magna. Ecology

71:2255–2268. doi: 10.2307/1938637

Howeth JG, Leibold MA (2010) Species dispersal rates alter diversity and ecosystem stability in pond metacommunities. Ecology 91:2727–2741. doi: 10.1890/09-1004.1

Jacob S, Chaine AS, Schtickzelle N et al (2015) Social information from immigrants: Multiple immigrant-based sources of information for dispersal decisions in a ciliate. Journal of Animal Ecology 84:1373–1383. doi: 10.1111/1365-2656.12380

Klüttgen B, Dülmer U, Engels M, Ratte HT (1994) ADaM, an artificial freshwater for the culture of zooplankton. Water research 28:743–746. doi: 10.1016/0043-1354(94)90157-0

Kot M, Lewis MA, van den Driessche P (1996) Dispersal data and the spread of invading organisms. Ecology 77:2027–2042. doi: 10.2307/2265698

Legrand D, Trochet A, Moulherat S et al (2015) Ranking the ecological causes of dispersal in a butterfly. Ecography 38:822–831. doi: 10.1111/ecog.01283

Lürling M, Roozen F, Van Donk E, Goser B (2003) Response of Daphnia to substances released from crowded congeners and conspecifics. Journal of Plankton Research 25:967–978. doi: 10.1093/plankt/25.8.967

Martorell C, Martínez-López M (2014) Informed dispersal in plants: Heterosperma pinnatum (Asteraceae) adjusts its dispersal mode to escape from competition and water stress. Oikos 123:225–231. doi: 10.1111/j.1600-0706.2013.00715.x

Michel J, Ebert D, Hall MD (2016) The trans-generational impact of population density signals on host-parasite interactions. BMC Evolutionary Biology 16:254. doi: 10.1186/s12862-016-0828-4

Michels E, Cottenie K, Neys L, Meester LD (2001) Zooplankton on the move: First results on the quantification of dispersal of zooplankton in a set of interconnected ponds. Hydrobiologia 442:117–126. doi: 10.1023/A:1017549416362

Pärt T, Doligez B (2003) Gathering public information for habitat selection: Prospecting birds cue on parental activity. Proceedings of the Royal Society of London B: Biological Sciences 270:1809–1813. doi: 10.1098/rspb.2003.2419

Poethke HJ, Kubisch A, Mitesser O, Hovestadt T (2016) The evolution of density-dependent dispersal under limited information. Ecological Modelling 338:1–10. doi: 10.1016/j.ecolmodel.2016.07.020

Ponchon A, Garnier R, Grémillet D, Boulinier T (2015) Predicting population responses to environmental change: The importance of considering informed dispersal strategies in spatially structured population models. Diversity and Distributions 21:88–100. doi: 10.1111/ddi.12273

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Skellam JG (1951) Random dispersal in theoretical populations. Biometrika 38:196–218. doi:

10.2307/2332328

Steiner CF, Stockwell RD, Tadros M et al (2016) Impacts of dispersal on rapid adaptation and dynamic stability of Daphnia in fluctuating environments. Proceedings of the Royal Society of London B: Biological Sciences 283:20152426. doi: 10.1098/rspb.2015.2426

Urban MC, Bocedi G, Hendry AP et al (2016) Improving the forecast for biodiversity under climate change. Science 353:aad8466. doi: 10.1126/science.aad8466

Van de Meutter F, Stoks R, De Meester L (2008) Size-selective dispersal of Daphnia resting eggs by backswimmers (Notonecta maculata). Biology Letters 4:494–496. doi: 10.1098/rsbl.2008.0323

Weider LJ, Hobæk A (1997) Postglacial dispersal, glacial refugia, and clonal structure in Russian/Siberian populations of the arctic *Daphnia Pulex* complex. Heredity 78:363–372. doi: 10.1038/hdy.1997.59

Tables

Table 1: Statistical test results for differences in *D. carinata* dispersal depending on food availability in patch 1 and food availability in patch 2. A generalised linear model was used with parameter estimates on the logit scale and binomial errors. Model variance was checked for overdispersion and did not violate standard GLM assumptions.

Parameter	Estimate (SE)	z stat	P value
Intercept	-3.455 (0.199)	17.35	<0.001
Food not available in patch 1	2.497 (0.228)	10.94	<0.001
Food not available in patch 2	-0.354 (0.316)	1.12	0.262
Food not available in patch 1 × *Food not available in patch 2*	0.375 (0.350)	1.07	0.283

Figures

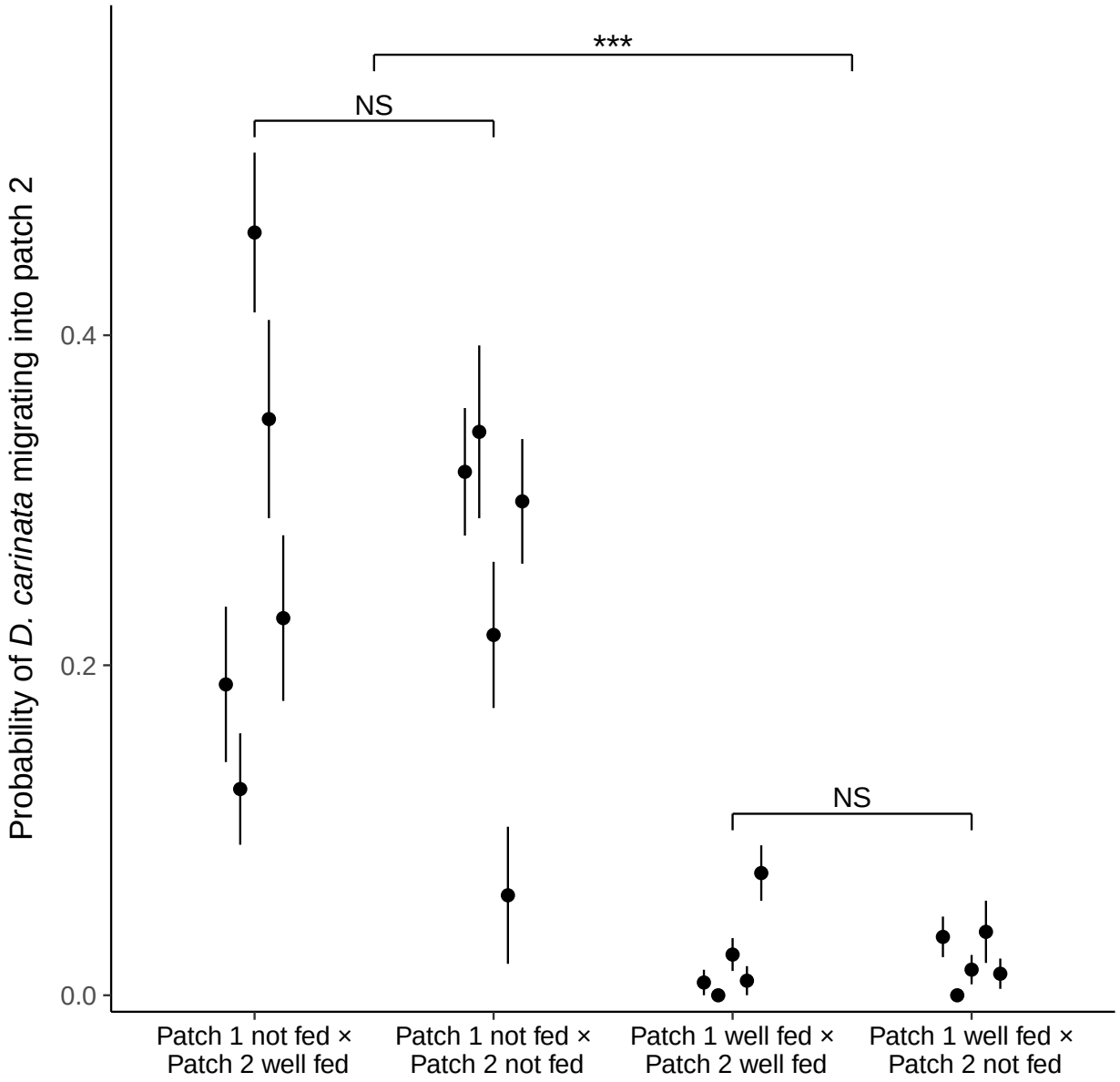

Figure 1: The effect of 96 hours of food deprivation on the probability of individual *D. carinata* dispersing, both with and without food available in patch 2 (n = 5 container pairs per treatment combination). Each point and line is given by the mean number of *D. carinata* individuals in patch 2 as a proportion of the total population size between the two patches ± SE (see Table A1 for precise results). Food availability in patch 1 alone was found to have a significant effect on the probability of an individual dispersing.