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Prerequisites for flying snails: external transport potential of aquatic snails by waterbirds

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Abstract. The widespread distributions of aquatic species often contrast with their limited ability to disperse by their own propulsion among wetlands isolated by land. Studies of the potential role of water birds as dispersal vectors have been focused mainly on internal transport (endozoochory). However, many anecdotal observations that small species adhere to flying birds also exist (ectozoochory). We addressed the hypothesis that ectozoochory may contribute to the widespread distributions of aquatic snails (Gastropoda) in several experiments. We tested the likelihood that snails would attach to mallards (*Anas platyrhynchos*) leaving macrophyte vegetation with high densities of 3 snail species. All species tested (*Gyraulus albus*, *Anisus vortex*, and *Radix balthica*) readily attached to the mallards' bodies. The rate of attachment was proportional to snail density, and the birds' feathers contained most snails. However, 2/3 of the snails detached when mallards subsequently walked for 3 m. Snails of 12 species attached within minutes to any surroundings available when floating in the water, a result indicating that active crawling onto birds may facilitate dispersal. Snails we attached deliberately to duck bills with mud could remain attached for up to 8 h. We measured desiccation tolerance of 13 common aquatic snail species. Almost all snail species survived 48 h of desiccation at 10 to 20°C. The ability to retain water did not differ between species with an operculum and species that form a mucus layer (epiphragm) in their shell openings. Our experiments indicate that aquatic snails possess a range of prerequisites for successful bird-mediated dispersal, but the capacity of snails (and other propagules) to remain attached during flight and successfully colonize new habitats upon arrival must still be assessed.

Key words: Gastropoda, ectozoochory, desiccation, dispersal, adhesion.

Biodiversity in isolated aquatic wetlands or on remote oceanic islands often includes species with limited ability to locomote (Page et al. 2007, Schabetsberger et al. 2009). Dispersal of these often small species by vectors, such as wind (anemochory), water (hydrochory), or larger, more mobile animals (zoochory) may explain their widespread distributions (e.g., Couvreur et al. 2005, Hogan and Phillips 2011). For many species that are restricted to aquatic habitats, this passive dispersal is essential for their persistence in wetland metapopulations that can cover multiple "islands in a sea of land" (Darwin 1909, p. 228).

Several potential vectors could help disperse aquatic species, and water birds were suggested as particularly suitable dispersal vectors long ago (Darwin 1859). Birds move quickly, are generally abundant, and migrate long distances between similar habitats. Observations of birds carrying smaller organisms have accumulated steadily since Darwin's time, and the number of publications on this subject has increased (Figuerola and Green 2002a, Green and Figuerola 2005). Terrestrial and water birds can transport plants, seeds, algae, and invertebrates internally if these organisms can survive passage through their digestive system (endozoochory) or externally if species adhere to their exterior during flight (ectozoochory) (reviewed by Maguire 1963, Sorensen 1986, Kristiansen 1996, Traveset 1998, Bilton

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et al. 2001, Figuerola and Green 2002a, Green and Figuerola 2005).

Brochet et al. (2010) regarded external transport of aquatic plants by adhesion as less important for dispersal than internal transport because they retrieved greater diversity and abundance of aquatic propagules from feces and lower guts than attached to birds. However, most knowledge of ectozoochory is still anecdotal (McAtee 1914, Cockerell 1921, Bondesen and Kaiser 1949, Roscoe 1955, Cotton 1960, Daborn 1976). Only some field observations (Vivian-Smith and Stiles 1994, Figuerola and Green 2002b, Frisch et al. 2007, Brochet et al. 2010, Raulings et al. 2011) and targeted experiments (Davies et al. 1982, Boag 1986, Barrat-Segretain 1996, Johnson and Carlton 1996) have been published.

Ectozoochory may be possible for aquatic snails (Gastropoda). Numerous anecdotal reports exist that snails adhere to birds (see review by Rees 1965), but only few experiments have been done to strengthen these observations (Darwin 1859, Boag 1986). Active dispersal by snails is limited to only few km/y (Kappes and Haase 2011), but dispersal by water birds may be an explanation for the generally rapid colonization of new suitable habitat by aquatic snails, their widespread distributions (Hubendick 1951), and the existence of multiple rapidly spreading invasive aquatic snail species (Dillon et al. 2002, Alonso and Castro-Diez 2008). The need to understand snail dispersal mechanisms is urgent because they are important dispersal vectors for human and livestock parasites (Brown 1978, Morley 2008).

We investigated the potential for ectozoochory in aquatic snails with 4 complementary experiments. First, we tested whether aquatic snails could attach to water birds and persist in this attachment. Second, we investigated whether snails stayed attached in drying mud on water birds. Third, we addressed the potential of snails to crawl onto birds by active movement. Last, we assessed the desiccation tolerance of 13 common aquatic snail species with various shell sizes and under various temperatures because desiccation tolerance strongly affects survival of aquatic species during external transport (Barrat-Segretain 1996, Figuerola and Green 2002a).

Methods

Transport experiment I

We tested the ability of snails to adhere to mallards (*Anas platyrhynchos*) in our bird facilities in Heteren, The Netherlands, in July 2009. We chose mallards because they are common, interact frequently with snails (Gruenhagen and Fredrickson 1990, Baldwin

and Lovvorn 1994), and adjust easily to captivity and experimental setups (Charalambidou et al. 2005, Soons et al. 2008). We ran a total of 48 trials with 12 different male mallards over a period of 4 d. We ran trials in the morning, early afternoon, and late afternoon. Each time, we took 4 mallards from the outdoor aviary and introduced them individually into 1 of 4 cages ($0.9 \times 0.7 \times 1.2$ m [l \times w \times h]). Cages were constructed of 10-mm-thick wood with 0.1-m-deep metal removable trays as bases.

One hour before each trial, we filled the trays to a depth of 0.05 m with water containing aquatic snails associated with a mixture of macrophytes dominated by *Elodea* sp. and *Lemna* sp. We collected this vegetation from a ditch at Driemond, The Netherlands (lat $52^{\circ}17'36''$ N, long $05^{\circ}01'13''$ E), <1 d before each trial, and held it overnight in aquaria under ambient temperature conditions. The snail species in this vegetation were *Gyraulus albus*, *Anisus vortex*, and *Radix balthica* (mean \pm SD densities = 13.0 ± 6.5 , 6.9 ± 3.7 , and 4.6 ± 5.7 snails/10 g plant material, respectively; $n = 15$). We defined snail size as the maximum measurable shell dimension (shell height for cone-shaped *R. balthica* and shell diameter for planorbid species; Gittenberger et al. 2004). Snail size was 4.1 ± 0.8 mm for *G. albus*, 3.6 ± 0.4 mm for *A. vortex*, and 4.5 ± 0.6 mm for *R. balthica* ($n = 10$ snails/species), and size was normally distributed.

We created 4 snail densities by adding 1.0, 2.0, 3.0, or 4.0 kg of the vegetation/snail mixture to the water in the trays. This procedure yielded linearly increasing snail densities of, on average, 1500, 3000, 4500, and 6000 snails/m² in a ratio of 3:4:8 (*R. balthica*:*A. vortex*:*G. albus*). Over the course of the experiment, we placed each mallard in a cage with each snail density once in a random block design over 48 trials.

For each trial, we kept mallards individually in the cages with vegetation for 60 min. Subsequently, we allowed them to exit the cage through a polyvinyl chloride (PVC) tunnel (0.41 m wide, 0.41 m high, 3.0 m long) covered by mesh wire. The tunnels connected the cages with vegetation to identical, but clean, cages where we examined the birds for adhering snails. We checked the tunnels for detached snails after each trial.

Before and after each trial, we inspected all mallards for snails with methods similar to those regularly used in field investigations (e.g., Vivian-Smith and Stiles 1994, Figuerola and Green 2002b, Brochet et al. 2010). First, we visually inspected the feet and bills of the mallards and rinsed their feet in clean tap water. Second, we brushed each bird with a soft shoe brush above an empty tray and checked for the presence of snails between its feathers. We sieved

the water used to rinse the feet and to wash the birds separately through a 1-mm-mesh sieve. We distinguished between those snails that remained attached to the birds (feathers, feet, or bill), those that detached while the bird walked through the tunnel (tunnel), and those that we detached during inspection of the bird for presence of snails in the final tray (tray).

Transport experiment II

We ran a 2nd transport experiment with *Potamopyrgus antipodarum* collected from the Ooijpolder, The Netherlands (lat 51°51'12"N, long 05°53'18"E). Mean snail size was 3.6 ± 0.7 mm (SD, $n = 10$). We mimicked snail ectozoochory that might occur after a mallard foraging bout in mud to test how long snails could potentially remain attached to birds after initial attachment. We used *P. antipodarum* as the focal species because of its relatively neutral characteristics for attachment by mud. It does not have a flat shell (like Planorbidae) or extensive mucous secretion (like *R. balthica*) that might facilitate attachment. We ran 25 trials, starting in the morning) over 4 d with 8 different male mallards. In each trial, we deliberately attached 10 snails to the bill of each mallard with an ~2- to 5-mm layer of mud. After attachment, we placed the mallards in clean cages (described above) without access to food or water. We checked the bills for detachment of snails at 30-min intervals over 8 h or until all 10 snails were detached from all birds during a trial.

Adhesion experiments

In May 2008 and 2009, we tested the readiness with which 11 freshwater and 1 marine snail species would attach to objects in their environment. We collected snails from their natural habitat in The Netherlands (for species and location details see Table 1; note that *P. planorbis* is in the table but was included only in the desiccation experiment described below). We held snails in aquaria filled with water from their sampling location at 15°C for no longer than 2 d before testing. For each species, we removed 100 snails from their aquarium and placed them in a 0.2 × 0.2-m plastic tray with 0.01 m of their natural water at 20°C for 5 min. At $t = 0$, we made sure all snails were detached, and then counted attached snails at 1-min intervals for 10 min.

Desiccation experiments

We monitored mass loss caused by evaporation of water and survival of 12 freshwater and 1 marine snail species in May 2008 and 2009. We collected snails from their natural habitat in The Netherlands

TABLE 1. Snail species per family, the year in which they were collected, their sampling location, presence of an operculum, the size range of tested individuals, and the shape of the shell.

Family	Species	Year	Latitude	Longitude	Location	Operculum	Size (mm)	Shape
Planorbidae	<i>Planorbis planorbis</i>	2009	52°8'39"N	5°13'6"E	Breukelen ditch	No	7–14	Flat
	<i>Planorbis carinatus</i>	2008	52°12'40"N	5°2'18"E	Loenen small pond	No	8–12	Flat
	<i>Gyraulus albus</i>	2008	52°17'36"N	5°1'13"E	Driemond ditch	No	2–3	Flat
	<i>Bathymphalus contortus</i>	2008	52°9'42"N	5°15'2"E	Loosdrecht ditch	No	2–4	Flat
	<i>Anisus vortex</i>	2009	52°17'36"N	5°1'13"E	Driemond ditch	No	4–8	Flat
Lymnaeidae	<i>Stagnicola palustris</i>	2009	53°8'22"N	6°1'40"E	Nijega ditch	No	9–19	Cone
	<i>Radix balthica</i>	2008	51°5'19"N	5°28'48"E	Meeuwen ditch	No	8–15	Cone
	<i>Lymnaea stagnalis</i>	2008	52°12'40"N	5°2'18"E	Loenen small pond	No	5–13	Cone
Valvatidae	<i>Valvata piscinalis</i>	2009	51°56'31"N	5°46'37"E	Driel ditch	Yes	2–5	Cone
	<i>Potamopyrgus antipodarum</i>	2008	51°51'12"N	5°53'18"E	Ooijpolder lake	Yes	2–4	Cone
Hydrobiidae	<i>Hydrobia ulvae</i>	2008	53°24'17"N	6°4'59"E	Paesens coast	Yes	3–5	Cone
	<i>Bithynia tentaculata</i>	2009	52°17'36"N	5°1'13"E	Driemond ditch	Yes	5–11	Cone
	<i>Bithynia leachii</i>	2008	52°3'33"N	5°10'14"E	Vechten ditch	Yes	2–5	Cone

(see Table 1 for species and location details). For each species, we divided 75 snails evenly among 3 desiccation treatments (ambient temperatures = 10, 15, or 20°C). We measured shell length and width as previously described, and weighed snails with a Sartorius Microbalance ME5 (resolution $d = 0.001$ mg; Sartorius AG, Goettingen, Germany) after removing outside moisture from their shells by rolling them in filter paper. Immediately after weighing them, we placed the snails individually in $10 \times 10 \times 10$ -mm cubicles in a $0.1 \times 0.1 \times 0.01$ -m tray covered with 1-mm mesh to prevent the snails from crawling out. We placed the trays over water in temperature-controlled aquaria to control humidity and held them at the appropriate temperature for 48 h. We monitored the air temperature in the trays with temperature loggers (Tinytag Talk 2, TK-4014-MED; Gemini Data Loggers [UK] Ltd., Chichester, UK) (mean \pm SD temperatures over 48 h = 10.2 ± 0.5 , 14.7 ± 0.6 , and 20.0 ± 0.6). In all cases, relative humidity of the air was between 80 and 85%. We measured snail mass after desiccation for 48 h and then resubmerged them in their natural water (taken from the sampling location) at 20°C. We assessed survival by monitoring movement over the next 7 d, and when in doubt, we checked by monitoring foot-retraction reactions after touch under a microscope.

Statistical analysis

For transport experiment I, we used linear regression to describe the relationship between the number of transported snails and snail density for all species together because of the limited available data (function *lm* in R; R Development Core Team, Vienna, Austria). For transport experiment II, we used the *lm* function to describe the relationship between the ($\log[x]$ -transformed) number of snails that remained attached to bills for ≥ 0.5 h and over time.

We tested the effects of snail size and possession of an operculum and desiccation temperature on survival with a generalized linear model (GLM) with binomial error distribution and logit link function (package *lmer* in R). We used viability of snails after 48 h as a binomial dependent variable and included snail size and desiccation temperature as covariates after centering (Raudenbush and Bryk 2002). We included operculum as a fixed factor, and year and snail species as random factors because we tested during 2 subsequent seasons, and the snail species had different size ranges (Table 1). We nested snail species in the fixed factor, operculum. We analyzed the effects of desiccation and shell size with separate linear models for each species. The % mass loss over

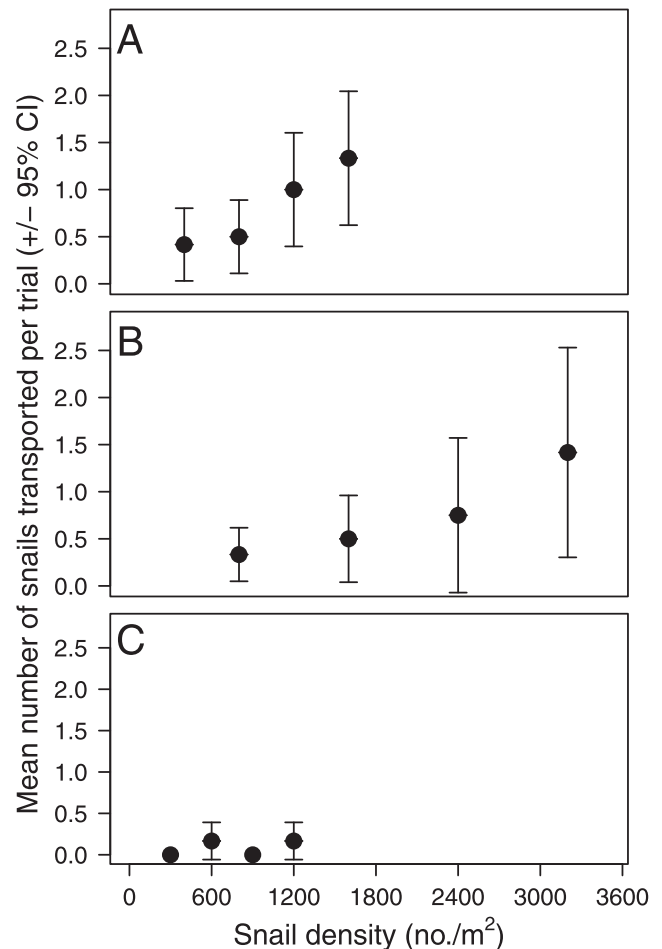


FIG. 1. Mean (\pm 95% CI, $n = 12$) number of snails transported from vegetation/trial as a function of snail density for *Anisus vortex* (A), *Gyraulus albus* (B), and *Radix balthica* (C).

48 h was the dependent variable and snail length and desiccation temperature were centered covariates.

Results

Transport experiments

In transport experiment I, all 3 snail species present in the vegetation were transported by mallards. Snails were transported out of the cages in 34 of 48 trials (71%). A linear increase in snail density resulted in a linear increase in total number of snails transported (linear regression calculated for all species pooled, $R^2 = 0.94$, $p < 0.01$). More *A. vortex* and *G. albus* were transported in total (found in the tray, in the tunnel, and on birds) than *R. balthica* (39 transported [0.33% of snails in the tray], 36 [0.23%], and 4 [0.04%]), respectively; Fig. 1A–C). Of the total number of snails transported, 65% detached either in the tunnel or in the tray, whereas 35% were still attached to the bird

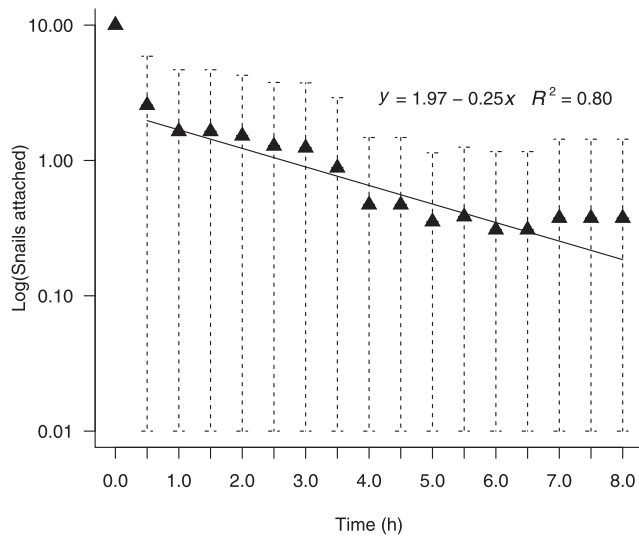


FIG. 2. Mean (± 1 SD) number of snails embedded in mud that remained attached to the bills of mallards (*Anas platyrhynchos*) over time. The number of snails decreased more than exponentially until the first check at $t = 0.5$ h, after which it followed an exponential decreasing function over the rest of time as indicated by the equation. Note log scale on y -axis.

upon examination. The feathers of the mallards contained almost $5\times$ more snails than the bill and feet together (23 vs 5 for all trials).

In transport experiment II, 74% of *P. antipodarum* individuals that were deliberately attached to the bills of the mallards with mud had detached before the first check after 30 min. The percentage of snails that detached thereafter declined exponentially over time (Fig. 2). Thirty-one snails (12.4%) remained attached in the dry mud for 3 h, and 3 (1.2%) remained attached for 8 h.

TABLE 2. The number of snails that attached to the tray during 10 min. The number is indicated in bold if no additional snails attached until termination of the experiment.

Species	Time (min)									
	1	2	3	4	5	6	7	8	9	10
<i>Radix balthica</i>	100									
<i>Bithynia leachii</i>	98	100								
<i>Lymnaea stagnalis</i>	45	95	100							
<i>Hydrobia ulvae</i>	90	93	98	99	100					
<i>Potamopyrgus antipodarum</i>	96	97	98	98	100					
<i>Stagnicola palustris</i>	66	82	83	88	93	100				
<i>Bithynia tentaculata</i>	60	89	93	94	94	94	94	95	96	98
<i>Bathymphalus contortus</i>	90	95	96	97						
<i>Gyraulus albus</i>	93	95	95	96	96	97				
<i>Valvata piscinalis</i>	41	66	75	86	90	94	96			
<i>Anisus vortex</i>	5	11	23	34	46	56	66	76	84	89
<i>Planorbis carinatus</i>	27	39	43	44	49	50	50	50	51	
Mean	68	80	84	86	89	91	92	93	93	94

Desiccation and adhesion experiments

In the adhesion experiment, >50% of individuals in 8 of 12 species adhered to their direct surroundings in <1 min (Table 2). In 10 of the 12 species (all except *A. vortex* and *P. carinatus*), >90% of all individuals adhered in <10 min.

In the desiccation experiment, over all snail species and all 3 temperature treatments, >50% of the 25 individuals in each temperature treatment survived. The only exceptions were that no *P. antipodarum* individuals survived the 20°C treatment and 48% of *A. vortex* survived this treatment. Mass loss and number of surviving individuals varied among species and shell sizes (Fig. 3, Table 3). Snail survival was negatively affected by the increase of temperature in the treatments (GLM, $z = -8.9$, $p < 0.001$, effect size = 1.7% less chance to survive if temperature increases by 1°C, based on all snail sizes and species pooled). Average mass loss (\pm SD) of snails was $7.0 \pm 7.7\%$ at 10°C, $11.6 \pm 10.3\%$ at 15°C, and $20.2 \pm 14.2\%$ at 20°C, calculated over all species (details per species in Table 3). The maximum mass loss before mortality differed among species (Fig. 3). Mass loss did not differ between species with and without opercula (GLM, $z = 0.017$, $p = 0.98$). Larger snails had a higher probability of surviving (GLM, $z = 2.7$, $p < 0.01$, effect size = 1.4% more chance to survive if shell size is 1 mm larger) and lost a smaller percentage of their initial mass, calculated over all species (details per species in Table 3).

Discussion

Waterbirds leaving macrophyte vegetation with snails carried a small percentage of these snails on their feathers, feet, and bills. The number of snails

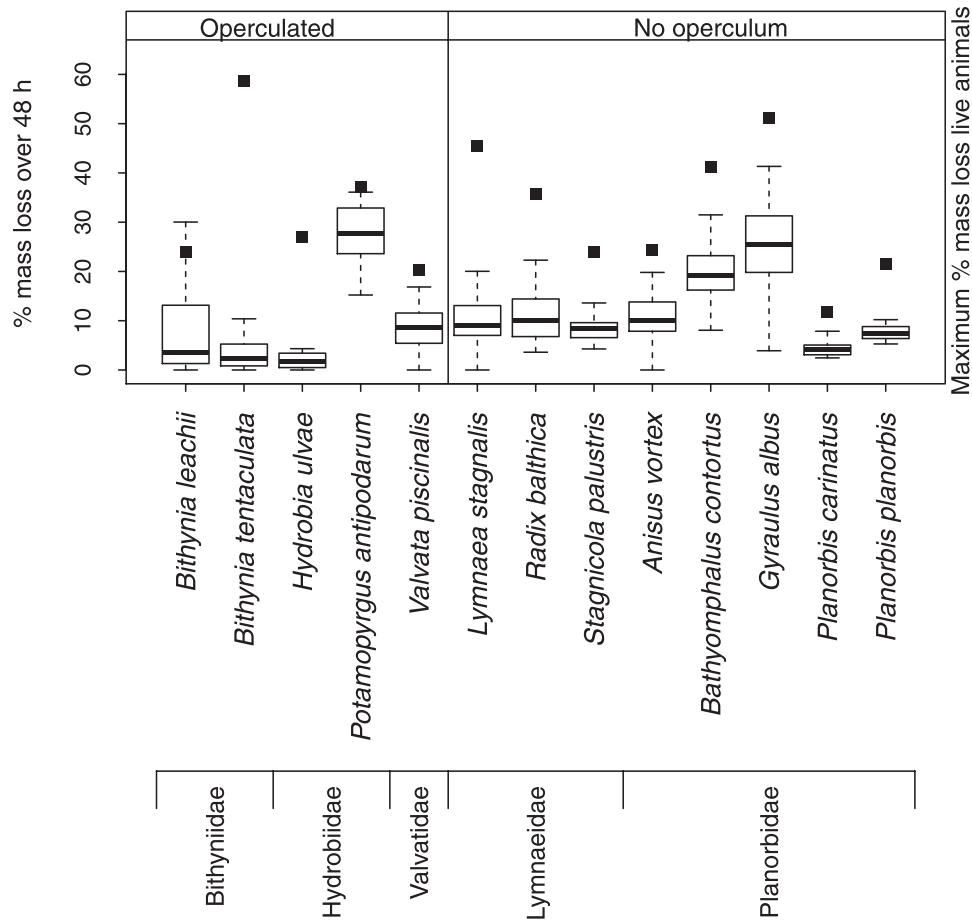


FIG. 3. Box-and-whisker plots for % mass loss of different species of snails during aerial exposure over 48h at 15°C. Species are ordered by families. Presence of an operculum is indicated for each species. Lines in boxes show medians, box ends show 25th and 75th percentiles, whiskers show 95% confidence intervals, and solid squares indicate the observed maximum % mass loss of live specimens, and thereby, the upper range of % mass loss during the experiments.

attached to their bodies increased proportionally with snail density, and snails adhering in drying mud could remain attached for several hours. Individuals belonging to many snail species actively attached to their available surroundings in minutes, and individuals in all snail species survived prolonged aerial exposure. Thus, initial attachment of snails to living waterbirds, subsequent adherence, and survival of desiccation during transport are unlikely to be limiting factors for ectozoochory of aquatic snails.

Initial attachment

At a density of 1000 snails/m², up to 10 snails attached per bird, but the number of attaching snails varied with snail species (Fig. 1A–C). Densities of snails in their natural environment can easily exceed several thousand/m² (Heitkamp and Zemella 1988, Gittenberger et al. 2004, Anders et al. 2009, Cadée 2011), so water birds that leave the water by walking

directly from vegetation may initially carry multiple snails. Snails probably attach both passively and actively.

Passive adhesion of snails on birds may be facilitated by the low mass of snails relative to the large contact surface of their shells. Many aquatic snails float at the water surface by adhering to the water surface film (e.g., Bimler 1976). Planorbidae have a flat shell shape, and their large surface-to-volume ratio facilitates flotation. This shell shape may assist passive adhesion to birds in a similar way. Our sample sizes were low, but the 2 Planorbidae species (flat shell shape) were carried more frequently than *R. balthica* (cone-shaped shell) (Fig. 1A–C).

In addition, snails attached rapidly to the surface of the tray, which was at that moment their only available surface (Table 2). This active behavior supports observations that snails crawl actively onto birds' feet and floating feathers (Darwin 1859, Boag 1986) and may lead to dispersal. Many egg-laying species lay

TABLE 3. The effect of shell length and desiccation temperature on its % mass loss over 48 h of desiccation. Coefficients (Coef) indicate the associated change in % mass loss given a change of 1 mm in shell length or 1°C in temperature. Full-model R^2 indicates the quality of model fit. Mean (± 1 SE) % mass loss and survival are indicated per species for the 3 temperatures. Bold indicates significant p -values.

Species	Shell length			Temperature			% survival						% mass loss			
	p	Coef	p	Coef	p	Coef	R^2	10°C	15°C	20°C	10°C	15°C	20°C	10°C	15°C	20°C
<i>Planorbis planorbis</i>	0.04	-0.7	<0.001	0.9		0.62		100	100	92	5.5 \pm 0.5	7.8 \pm 0.4	15.0 \pm 0.9			
<i>Planorbis carinatus</i>	0.47	0.3	0.11	0.1		0.04		100	100	100	3.6 \pm 0.5	4.4 \pm 0.3	4.5 \pm 0.3			
<i>Gyraulus albus</i>	0.16	-8.2	<0.001	1.4		0.18		100	68	56	12.3 \pm 2.2	25.0 \pm 2.2	26.3 \pm 3.4			
<i>Bathymphalus contortus</i>	<0.001	-11.0	<0.001	2.5		0.74		100	92	72	6.3 \pm 0.9	19.5 \pm 1.4	30.0 \pm 2.4			
<i>Anisus vortex</i>	0.85	0.1	<0.001	1.6		0.54		68	60	48	2.3 \pm 0.8	12.1 \pm 1.4	18.0 \pm 1.2			
<i>Stagnicola palustris</i>	0.40	-0.2	<0.001	1.2		0.59		76	80	52	6.2 \pm 0.8	8.0 \pm 0.6	17.9 \pm 0.8			
<i>Radix balthica</i>	<0.001	-1.6	<0.001	1.9		0.72		100	100	100	6.1 \pm 1.0	10.8 \pm 1.0	25.1 \pm 1.2			
<i>Lymnaea stagnalis</i>	0.04	-1.0	<0.001	1.4		0.40		100	96	84	10.5 \pm 1.1	10.2 \pm 1.1	23.4 \pm 1.5			
<i>Valvata piscinalis</i>	<0.01	-3.0	<0.001	1.2		0.42		84	88	52	8.3 \pm 0.6	8.3 \pm 0.8	20.6 \pm 1.9			
<i>Potamopyrgus antipodarum</i>	0.01	-5.0	<0.001	3.3		0.72		92	68	0	18.8 \pm 2.2	27.9 \pm 1.4	50.0 \pm 0.9			
<i>Hydrobia ulvae</i>	0.21	-1.3	<0.001	0.7		0.39		100	100	100	2.5 \pm 0.6	2.0 \pm 0.4	10.1 \pm 0.9			
<i>Bithynia tentaculata</i>	<0.01	-2.6	0.06	0.5		0.19		100	100	72	3.1 \pm 2.2	3.5 \pm 0.7	10.1 \pm 2.7			
<i>Bithynia leachi</i>	<0.01	-4.4	0.04	0.7		0.13		100	60	60	5.1 \pm 1.1	11.7 \pm 3.4	11.3 \pm 2.2			

their egg capsules on substrates (Gittenberger et al. 2004) like the feet of birds or produce sticky mucous layers (Darwin 1859, Boag 1986, Smith 2002, Gittenberger et al. 2004) that may facilitate attachment. Both passive and active attachment of snails may facilitate their initial attachment.

Prolonged adhesion

After initial attachment, many snails detached rapidly from the mallards in both transport experiments (Fig. 2). This result suggests that ectozoochorous dispersal will usually result in only short-distance dispersal and confirms the results of previous experiments in which snails adhered for only 15 min to duck feathers during simulated flight (Boag 1986). Snails attached by drying mud probably have the greatest potential for long-distance dispersal. Most snails that remained attached during the first 30 min (during which the mud dried) detached quickly, but some snails stayed attached for up to 8 h. The mallards in the experiment did not actively clean the snails from their bills, although birds could move freely in their cages. Therefore, the snails that remained attached for hours were released after birds submerged their bills, analogous to arrival in another aquatic habitat (Malone 1965).

Facilitation of ectozoochory by mud on waterbirds has been suggested for plant seeds (Barrat-Segretain 1996 and references therein), and both seeds and aquatic invertebrates have been retrieved from mud transported by boars (*Sus scrofa*) (Vanschoenwinkel et al. 2008). While autonomous attachment might result in short (<1 h) attachment (Boag 1986), longer adhesion may be possible with mud as an adhesive. This idea is supported by a previous observation of Figuerola and Green (2002b) who noted that birds in a muddy habitat carried more propagules than those in a sandy habitat.

Propagule survival

The high survival rate of all snail species tested during the desiccation experiments suggests that aerial exposure does not prohibit snail dispersal. Many aquatic snails live in habitats that dry occasionally, such as temporary freshwater ponds or tidal areas, and are adapted to desiccation (Wiggins et al. 1980). Shells can be permeable to water (Van Aardt and Steytler 2007), but most water loss occurs through the shell aperture and from the surface of the foot (Storey 1972). Prosobranchs reduce such losses by closing their aperture with an operculum (Gibson 1970) and pulmonate species by producing a mucous layer (epiphragm) (Storey 1972, Eckblad 1973, Jokinen 1977). Both adaptations allow survival in extreme

conditions, such as drought or freezing in winter, when most snail species go into dormancy (aestivation; Storey 1972, Jokinen 1977, Frentrop 1998a, b).

Our 48-h desiccation experiments indicate that water loss does occur during short-term desiccation, but that the desiccation is mostly nonlethal (Fig. 3, Table 3). Water loss and survival did not differ between operculated snails and snails with an epiphragm. However, smaller snails lost a larger percentage of their body mass and had lower survival than large snails, a common pattern for small aquatic species (Ricciardi et al. 1995, Paukstis et al. 1999, Facon et al. 2004). Thus, small propagules are generally more successfully transported and are found more often between feathers than large snails (Sorensen 1986, Brochet et al. 2010), but larger snails may have higher survival. Together, our results indicate that snails of intermediate size (3–5 mm) might be most suitable for transport because this size class attached readily during transport experiments and survived desiccation.

Mass loss of snails in our desiccation experiments varied with temperature (Table 3), and varied with humidity in experiments done by Heitkamp and Zemella (1988). Interesting in this respect is that Winterbourn (1970) found that *Potamopyrgus antipodarum* could survive for up to only 30 hours in dry situations, but survival >30 d was possible in damp situations. Because migratory birds also face dehydration risks during migratory flight (Gerson and Guglielmo 2011) and may opt for flight routes and conditions that minimize water loss (Klaassen 2004), potential stowaways could be facilitated by this higher relative humidity.

Conclusion

Aquatic snails can attach to living mallards passively or actively, remain attached in drying mud for several hours, and survive long periods of aerial exposure. Therefore, ectozoochorous dispersal by waterbirds might be a plausible explanation for the wide distributions of many snail species. Whether long distance dispersal of snails truly occurs in natural situations remains a challenge for future research. However, our study shows that many aquatic snail species have the necessary prerequisites for successful dispersal.

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