Waterbird-mediated passive dispersal is a viable process for crayfish (*Procambarus clarkii*)

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Abstract Human transport and active dispersal of the red swamp crayfish (*Procambarus clarkii*) contribute to its rapid spread. However, some small aquatic organisms can be transported by birds. We made two hypotheses related to waterbird-mediated passive dispersal of juvenile crayfish. The first is that, depending on water depth, recently hatched crayfish can attach to ducks, initiating passive external transport (i.e., ectozoochory). The second is that recently hatched crayfish can survive bird flight, being affected by crayfish features, flight distance, and environmental conditions. A first experiment tested the attachment of juvenile crayfish to ducks at different water depths by using a freshly dead duck and tanks with crayfish.

Another set of three experiments tested crayfish survival during air transportation. To simulate bird flight, we first used a vehicle moving at bird flight speed, and we then used trained pigeons. Several flight distances, environmental conditions, and crayfish sizes were tested. Our results showed that juvenile crayfish were capable of clinging to duck feathers and were transported when ducks were removed from the water. Furthermore, some juveniles of *P. clarkii* were able to survive long-distance transport when suspended outside a moving vehicle or when transported by birds. The probability of success was affected by water depth, crayfish size, distance travelled, and relative humidity. Our results support the occurrence of passive transportation of this invader by means of attachment to birds. These findings indicate that waterbird-mediated passive dispersal should be taken into account to explain *P. clarkii*'s rapid spread and should be considered when managing its invasions.

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Introduction

The red swamp crayfish (*Procambarus clarkii,* Girard) is a widespread invader of freshwater ecosystems. Once established, the species causes negative impacts

on indigenous crayfish and on a number of other aquatic organisms (Geiger et al. 2005; Gherardi 2007; Holdich et al. 2010). Nonetheless, in invaded areas, several predators have changed their diets to establish crayfish as a major item (Adrian and Delibes 1987; Correia 2001), indicating a possible positive effect for some native species. This species also has a well-known negative impact on economic activities, particularly rice crops (Anastácio et al. 2000, 2005a, b), although economic benefits are also obtained by its commercial exploitation both in its area of origin in the southeast of North America and in several invaded regions (e.g., Spain and China) (Huner 1995). Since its initial introduction to southern Spain during the 1970s (Habsburgo-Lorena 1978), the species is now established across almost the entire Iberian Peninsula (Gutiérrez-Yurrita et al. 1999) and in many other European countries (Souty-Grosset et al. 2006).

Diffusion dispersal is considered to occur primarily between adjacent, or nearly adjacent, environments (Davis and Thompson 2000). In the case of freshwater crayfish, these nearby habitats may include isolated water habitats, implying some sort of active overland dispersal (Cruz and Rebelo 2007; Siesa et al. 2011). Active overland dispersal by freshwater invertebrates is most obvious and best documented among winged insects, although crayfish have also been observed dispersing terrestrially (Penn 1943; Grey and Jackson 2012). The rapid diffusion of *P. clarkii* following its establishment in a new region is attributed to its active dispersal capabilities (Barbaresi and Gherardi 2000), but aquatic dispersal has been the focus of most studies. Like other aquatic crustaceans, this species can survive out of water for relatively long periods of time, namely during post-reproductive migrations (Penn 1943).

Human commercial activities, specifically aquaculture, legal or illegal stocking, live food trade, and aquarium and pond trade (Lodge et al. 2000; Chucholl 2013), have led to the deliberate introduction of *P. clarkii* over long distances (e.g., Capinha et al. 2013). Green and Figuerola (2005) defined long-distance dispersal (LDD) of aquatic invertebrates as their overland dispersal between wetlands separated by at least 10 km. LDD can be viewed as movement between environments that are usually separated by a barrier of some sort, a process that could be termed *saltation dispersal* or *punctuated dispersal* and that is facilitated by humans (Davis and Thompson 2000).

However, short-distance overland dispersion mechanisms may be important for the regional speed of the invasion front of this species. Irrespective of the dispersal mechanism, it is known that *P. clarkii's* expansion is rapid and that large areas of the planet are still available for invasion (Capinha et al. 2011). Therefore, several countries have adopted legislation regarding the control of its spread, relying on the successful management of human activities and sometimes disregarding the possibility of other relevant mechanisms of dispersion.

It has long been recognized that waterbirds may be an important vector for dispersal of aquatic organisms (Darwin 1859; Ridley 1930). In fact, propagules of aquatic organisms, such as seeds of aquatic plants, diapause eggs of invertebrates, and spores of freshwater algae, can be transported in waterbirds' guts (endozoochory or internal dispersal) (Charalambidou and Santamaría 2002) or attached to their bodies (ectozoochory or external dispersal) (Darwin 1859; Ridley 1930). These processes are considered to have a major impact on the metapopulation dynamics and gene flow of many aquatic organisms (Green and Figuerola 2005). Passive external transport is achieved by the translocation of individuals that become attached to mobile animal vectors such as waterfowl or other aquatic vertebrates (Bilton et al. 2001). The Anatidae (ducks, geese, and swans) are of particular importance for the dispersal of several aquatic organisms because of their abundance, widespread distribution across the world's wetlands, and the capacity of several species for long-distance movements (Del Hoyo et al. 1992). Actually, the literature suggests that the Anatidae play an important role in the population and community ecology of aquatic invertebrates and plants by acting as vectors of passive dispersal (Green et al. 2002). Although the occurrence of waterbird-mediated dispersal is recognized for many small aquatic organisms, the ectozoochory of large crustacean species that have small hatchlings, such as *P. clarkii*, deserves further attention. Since it is very difficult to obtain direct field data on low-probability dispersal events, we adopted an experimental approach in which we analyzed different components of the dispersion process. Under this context, our objectives were to assess whether *P. clarkii* juveniles can cling to waterbirds and survive bird flight. We further explored which types of factors affect these processes.

Methods

Previous literature indicated a higher likelihood of transport for smaller organisms (Boag 1986; Figuerola and Green 2002; De Bie et al. 2012). Therefore, we collected juvenile *P. clarkii* using dip nets (1 mm mesh size) dragged in the shallow margins of rice field irrigation channels in Paul de Magos, Portugal (38°58′N, 8°45′W). Since experiments were not simultaneous, we were limited by the availability of recently hatched crayfish at the time of each experiment and always used the smallest available cohort. After capture, animals were transported to the laboratory and kept for 3 days in aerated tanks at densities ranging from approximately 200–400 ind. m^{-2}.

Estimating the probability of clinging to a duck

We performed an experiment with a freshly dead domestic muscovy duck (*Cairina moschata*). This aimed to quantify the probability of passive external transport of juvenile crayfish on duck feathers at shallow water depths. Shallow water was chosen since feeding activity of mallards (*Anas platyrhynchos*), one of the most common ducks in *P. clarkii*'s invasive range, mostly occurs in shallow areas (Jorde et al. 1983). We used three tanks (57 × 43 cm wide and 39 cm high) that differed in water depth, with 1, 5, and 10 cm, respectively. Each contained 98 juvenile crayfish with an average total length ($\overline{TL}$) of 11.94 mm (± 2.55 SD), corresponding to a density of 400 juveniles per m^2, which is high but within the literature range for juveniles in invaded areas (Harper et al. 2002). In the experiment, we immersed the duck in a tank for a period of 90 s. Then the duck was passed to another tank without crayfish, and the number of crayfish transported among tanks was annotated. We also annotated if any crayfish fell during transport. Since we were simply testing whether the crayfish would hang from a duck flying away from the water, the distance among tanks was only 5 m. Altogether 130 duck movements between tanks were conducted for the water depths of 1 and 10 cm and 80 movements for the water depth of 5 cm.

Survival under simulated flight conditions

To find the order of magnitude of the distances we should use in a set of experiments with actual bird flight, we first quantified juvenile crayfish survival during a simulation using a moving vehicle. In this experiment, we mimicked both pigeons' flight speed (45–73 km h^{-1}) (Wiltschko et al. 2007) and ducks' flight speed (60–78 km h^{-1}) (Welham 1994) using individual plastic mesh bags (2 mm mesh, 2 × 8 × 2 cm) hanging out of the car. Control animals were kept in the same type of bags in water inside the car.

In the first approach, a set of 30 juvenile *P. clarkii* with a $\overline{TL}$ of 22.56 mm (±2.83 SD) were hung inside mesh bags out of a vehicle moving at a constant speed of 70 km h^{-1} at an air temperature of 17 °C and a relative humidity of 36 %. After 10, 30, and 50 km, we verified how many were still alive. A control group of 10 crayfish was used. We performed a second experiment in which we counted the number of survivors in sets of crayfish in individual mesh bags that were removed at fixed distances. In this experiment, we used 45 juvenile *P. clarkii* ($\overline{TL}$ = 25.38 mm ± 3.18 SD), and the car was driven at a constant speed of 70 km h^{-1} at an air temperature of 18 °C and a relative humidity of 47 %. At distances of 25, 50, 75, 100, and 150 km, one set of 9 crayfish was removed, and the number of animals alive was counted. A control group of 9 crayfish was used.

After the experiments with the car, we also performed three runs of an experiment using pigeons to quantify crayfish survival during bird flight. Homing pigeons were used because in this way we could test releases from fixed distances, knowing that the animals could be easily recovered. We tied a small plastic mesh bag (same as above) containing one crayfish to each pigeon's identification ring. Ten bags with juveniles were kept in the water as controls during each run.

In the first run of the experiment, we released 30 pigeons with juvenile *P. clarkii* ($\overline{TL}$ = 17.91 mm ± 2.52 SD). We released 15 pigeons at 64 km and 15 pigeons at 112 km from the dovecote. In the second run of the experiment, three distances were tested: 3, 5, and 11 km. For each distance, 10 pigeons were released, each with a crayfish in a mesh bag ($\overline{TL}$ = 9.39 mm ± 1.35 SD). In the third run of the experiment, we used juvenile *P. clarkii* with a $\overline{TL}$ of 10.88 mm (±2.10 SD) on distances of 5, 10, and 20 km. However, due to unstable weather conditions during this run, we only obtained data for 8 pigeons. During all the runs, we recorded average temperature,

relative humidity, time of release, and time of arrival, as well as the travel time. Crayfish survival was checked both at the end of the experiment and 12 h after.

Estimating the number of juvenile crayfish transported for each distance

To estimate the level of impact of the ectozoochory for *P. clarkii* dispersal, we used our own data on field abundances of juveniles in a Portuguese freshwater marsh—Paúl do Taipal (40°10′N, 8°41′W)—during the early years of invasion (Anastácio and Marques 1995). Data on the abundance of ducks on this marsh are also available, although not for the same year, and a very conservative value was used since duck densities were frequently much higher in this location (Costa and Guedes 1994). A 1.5 km flight distance was used since it is above the normal overland crayfish walking distance and is sufficient to overcome a small dispersal barrier. In fact, this distance may be sufficient to reach another river basin, which may occur in some low-order streams that are very close to each other. To estimate the feasibility of long-distance dispersal, i.e., over 10 km (Green and Figuerola 2005), we also performed calculations for 10, 20, and 50 km. For simplicity, this was done assuming the same number of birds traveling over these distances.

Statistical analysis

In order to analyze the probability of *P. clarkii* survival during bird flight, a binary logistic regression was performed using the backward stepwise (Wald) variable selection method. As covariates, we included crayfish total length (mm), air temperature (°C), relative humidity (%), flight duration (minutes), and flight distance (km). The results regarding the transport between adjacent tanks using a duck were analyzed using a chi-square test for a contingency table. All analyses were performed using IBM PASW version 18. Survival was estimated by the proportion of individuals alive.

Results

Estimating the probability of clinging to a duck

Several juveniles were transported, and numerous juveniles were observed in the water in the destination tank at a distance of 5 m between tanks. No crayfish fell while in transit between the tanks. We recorded simultaneous attachment of more than one juvenile to the duck on 31 occasions at the 1 cm depth, on 9 occasions at 5 cm, and on 10 occasions at 10 cm. These values represent, respectively, a 24, 11, and 8 % probability of attachment to the duck. Water depth affected the proportion of juveniles transported on the duck's feathers ($X^2 = 14.51$, $df = 2$, $N = 240$, $P < 0.001$). Figure 1 shows a clear decrease in transport with increasing water column depth.
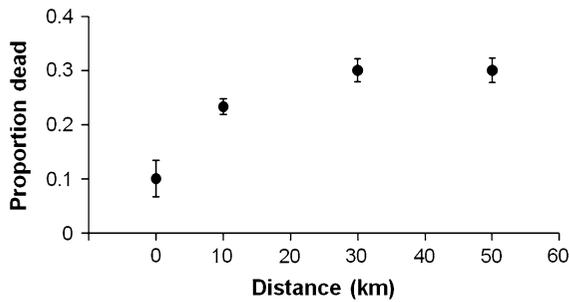
Survival under simulated flight conditions

In the first experiment, results showed a very high survival rate of crayfish after 50 km at a speed of 70 km h^{-1}. We found that 70 % of the crayfish were alive after the end of the experiment, a slightly lower percentage than the control group (90 %). Figure 2 shows that for a maximum distance of 50 km, the cumulative proportion of dead crayfish increased sharply during the first 10 km. In the second experiment, only one crayfish died after 100 km, and no deaths were recorded for the remaining distances, including the longest, 150 km (Fig. 1).

Our results with trained pigeons revealed that crayfish were able to survive out of water under
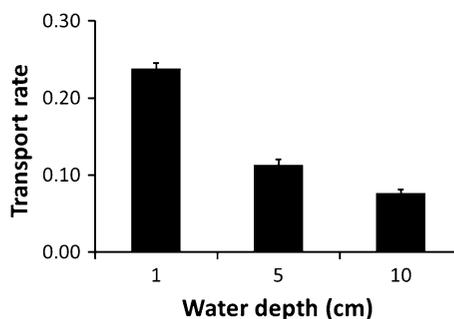
Fig. 1 Juvenile crayfish attachment and transport by a dead duck, during experiments at three different water depths. The proportions are the number of crayfish transported divided by the number of duck movements performed; 95 % confidence intervals are presented

Fig. 2 Cumulative proportion of dead crayfish in the first experimental study simulating bird flight conditions using a car
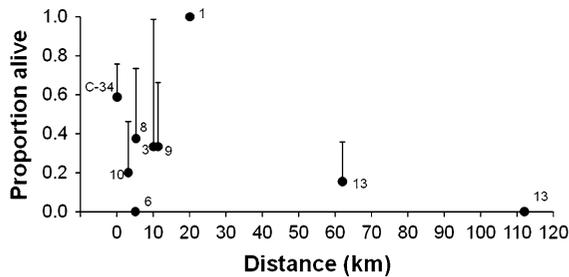
Fig. 3 Proportion of crayfish survival during experiments with homing pigeons carrying juvenile crayfish. The numbers next to the *dots* are the number of pigeons returning to the dovecote for each distance, C means control

Table 1 Variables that integrate the equation according to a binary logistic regression to predict crayfish survival during bird flight

	B	SE	Wald	df	Sig.	Exp(B)
Relative humidity (%)	0.017	0.009	3.050	1	0.081	1.017
Distance travelled (Km)	−0.063	0.027	5.514	1	0.019	0.939
Crayfish total length (mm)	0.365	0.177	4.248	1	0.039	1.440
Constant	−4.628	1.747	7.018	1	0.008	0.010

extreme conditions during long-distance transport by a vector (Fig. 3). The binary logistic regression performed using trained pigeons' data showed that flight distance, crayfish total length, and relative humidity were included in the model explaining crayfish survival rate (Table 1). Crayfish total length and relative humidity had positive effects on survival,

Table 2 Variables that do not integrate the equation and seem to have no connection to the predicted crayfish survival during bird flight, according to a binary logistic regression

	Score	df	Sig.
Variables			
Temperature (°C)	0.315	1	0.574
Flight duration (min.)	0.003	1	0.960
Overall statistics	0.346	2	0.841

Table 3 Model performance according to a binary logistic regression (see Table 1) predicting crayfish survival during bird flight

	Predicted survival		
	Dead	Alive	Percentage correct
Observed survival			
Dead	48	7	87.3
Alive	11	14	56
Overall percentage			77.5

while flight distance had a negative effect. Temperature and flight duration had no influence on the survival rate, so they were not integrated in the equation (Table 2). Overall, model predictions were 77.5 % correct (Table 3). The Hosmer and Lemeshow chi-square test for the overall fit of the binary logistic regression was not significant ($X^2 = 5.876$, $df = 8$, $P = 0.661$) therefore indicating that the model adequately fits the data.

From the binary logistic regression results, the probability (P) of juvenile crayfish survival during transport by a bird is given by the equation:

$$P = \frac{1}{1 + e^{-(-4.628 + 0.017*H - 0.063*D + 0.365*L)}}$$

in which H is the relative humidity expressed in % saturation, D is the distance travelled by the bird expressed in Km, and L is the total length of the crayfish expressed in mm.

Estimating the number of juvenile crayfish transported for each distance

We estimated a transport of 7.4 juveniles each day to distances of 1.5 km (Table 4). Using the same rationale, our calculations for 10, 20, and 50 km distances resulted, respectively, in 6.6, 5.4, and 1.7 individuals

Table 4 Estimated probability of successful transport of *Procambarus clarkii* juveniles by ducks on a typical freshwater marsh site during the beginning of the invasion

Element to consider	Value	Notes
Relative humidity, RH (%)	73	October value of the climate normal for Coimbra 1961–1990 ftp://dossier.ogp.noaa.gov/GCOS/WMO-Normals/RA-VI/PO/08549.TXT()
Crayfish size (mm)	14	October 1991 average field value for the Paúl do Taipal
Water depth (cm)	10	Mallard feeding is mostly in shallow areas (Jorde et al. 1983)
Distance (km)	1.5	Median flight distance for mallards (Davis and Afton 2010). Also within the 1–2 km range by Legagneux et al. (2009)
Number of ducks in the area	325	Ducks in Paúl do Taipal, Portugal, October 1992 (Costa and Guedes 1994). Values are frequently larger
Juvenile crayfish density (ind./m^2)	136	October 1991 field values from Paúl do Taipal (Anastácio 1995)
Probability for 1 duck at 400 juvs/m^2 and 10 cm depth	0.080	Values obtained for a duck, immobile for 90 s
Daily probability of taking the vector	8.840	Number of ducks in the area × Probability for 1 duck at 400 juvs/m^2 and 10 cm depth × Crayfish density/400
Probability of surviving the flight	0.836	$1/(1 + \mathrm{EXP}(-(-4.628 + 0.017 \times \mathrm{RH} - 0.063 \times \mathrm{Distance} + 0.365 \times \mathrm{Crayfish\ size})))$
Daily probability of passage	7.390	Daily probability of taking the vector × Probability of surviving the flight
Weekly probability of passage	51.729	
Monthly probability of passage	221.698	

transported each day, which indicate a tangible possibility of transport.

Discussion

Our experiments demonstrated that crayfish juveniles are able to attach themselves to a duck's feathers and that there is a very high capacity for crayfish survival out of water under flight conditions. In fact, juvenile crayfish were able to survive transport distances over 150 km outside a moving vehicle. These results are an approximation of the desiccation survival rates that could be expected during bird flight and highlight that desiccation will not limit long-distance transport among river basins. Moreover, these results are also relevant to human-aided invasions. They show that a vehicle such as a car or a boat that is transported between two river basins is likely to be a vector of the species if accidentally contaminated with juvenile crayfish. In fact, for other freshwater species such as the zebra mussel (*Dreissena polymorpha*), boats are indicated as the main driver of dispersal when compared with transport by waterfowl (Johnson and Padilla 1996). Recent studies have also confirmed that both cars and boats are possible mechanisms of dispersal for nonquiescent forms of other freshwater invasive animal species (Waterkeyn et al. 2010).

Waterbirds can transport plants and invertebrates between wetlands (Figuerola and Green 2002; Green et al. 2002; Brochet et al. 2010). Vivian-Smith and Stiles (1994) reported seeds adhering to the feathers and feet of 28 out of 36 geese and ducks, suggesting that external transport may be an important process, at least in some areas. Darwin (1859) proved the adhesion of snails to a waterbird, and the feasibility of mollusk overland transport has been further tested and confirmed by authors including van Leeuwen and van der Velde (2012), Alonso and Castro-Díez (2012), and Tarnowska et al. (2012). Other studies demonstrated the ability of amphipods (Segerstrale 1956), cladocerans (Matkovich, pers. observ. in Makarewicz et al. 2001), and freshwater shrimps (Banha and Anastácio 2012) to cling to waterbirds such as ducks. Like in those studies of a range of species, our results demonstrate that clinging of crayfish juveniles to duck's feathers is possible.

Procambarus clarkii survival during bird flight was negatively affected by distance and positively affected by crayfish total length. In spite of this, the very small size of juveniles could explain the large attachment rates to the feathers during the experiments using a

dead duck. Passive aquatic dispersers seem to be limited by size (De Bie et al. 2012), and there is some evidence that smaller propagules and those with hooklike structures are more likely to be attached to waterbird plumages (Figuerola and Green 2002). Studies on ectozoochory of aquatic organisms refer predominantly to transport of small individuals, e.g., of freshwater gastropods up to 2.5 mm (Boag 1986). Notably, some works indicate transport of larger animals, such as Bivalvia on waterfowls' feet (Green and Figuerola 2005), Gastropoda (Wesselingh et al. 1999), or freshwater amphipods of the genus *Gammarus* (Segerstrale 1956; Peck 1975; Daborn 1976; Swanson 1984). Figuerola and Green (2002) and Vanschoenwinkel et al. (2008) mentioned that size, shape, hardness, and resistance to desiccation affect the dispersal of propagules. It is therefore likely that those factors can also influence *P. clarkii* survival during bird-mediated transport.

Anecdotal references to how long freshwater crustaceans survive attached to flying birds mention "a few hours" in the case of the amphipod *Hyalella azteca* (Rosine 1956), 50 km in the case of the Cladocera *Cercopagis pengoi* (Makarewicz et al. 2001) and 400 m in the case of *Gammarus lacustris* (Swanson 1984). Since our experiments using moving vehicles mimicked pigeons' and ducks' flight speed, we conclude that a small fraction of juvenile crayfish can resist desiccation during bird flight for up to 129 min or 150 km. Actually, the vast majority of waterfowl movements occur over short distances, with only a few flights over long distances. Most movements are of <5 km, and these are usually related to foraging and maintenance behavior within a wetland or group of wetlands (Roshier 2008). Mallard flight distances have been analyzed by several authors, who obtained values of 2.1 km for average daily one-way distance flights to feeding areas (Devoucoux 2010), 1–2 km for foraging distances away from roosts (Legagneux et al. 2009), and 1.5 km for median female mallard movement distances (Davis and Afton 2010). Since short-distance movement largely prevails over long distance, to make projections of the potential impact of waterfowl on the dispersal rate of *P. clarkii*, we started by making calculations for these distances. However, transport by ducks will only be relevant for species dispersal if the distances analyzed are above the terrestrial walking capabilities of adult *P. clarkii*. A previous study (Anastácio 2010) showed that adults can survive out

of water for periods up to 16.5 h at 16 °C and 53 % relative humidity, and the overland walking speed of adults is approximately 40 m h^{-1} (pers. obs.). This means that *P. clarkii* exiting water and continuously walking in the same direction would reach maximum distances of 660 m from their point of origin. The average flight distance for waterfowl is higher than this value and occasionally much larger distances are covered. We therefore conclude that ducks could effectively contribute to the spread of *P. clarkii*.

It is important to notice some issues with the values estimated in Table 4, i.e., 7.4 individuals/day^{-1} for 1.5 km. One issue regards the assumption that survival during flight, as simulated using the pigeons, is equivalent to survival when wild ducks are the vector. The major problem with this assumption is related to the possibility of live crayfish falling off the duck vector; this could not happen during the experiments with the pigeons since the crayfish were inside a mesh bag. In a small number of replicates of the experiment with the duck, we could see crayfish clinging to the chest feathers or to its legs, but no quantification was possible. More complex experiments involving birds would clarify this further, and we believe that the actual value for the successful dispersal of crayfish by birds may be lower than we calculated. The second problem regarding the dispersal is that we are dealing with juvenile crayfish, which would have to survive to adulthood in the new area and find a mate in order to establish a new population. When we consider a dispersal radius of 1.5 km, it does not mean that all the crayfish are dispersed to the same location, although some locations are most often visited by the ducks. Despite the simplifications in our calculations, the values obtained can be regarded as a clear indication for an enhancement of *P. clarkii*'s dispersion capabilities even if we decrease these values by an order of magnitude. Following the above argument, we would still have a transport of more than 5 animals each week over a 1.5 km distance.

A very short description of an ectozoochory experiment demonstrated that the initial life stages of the invasive bivalve *Dreissena polymorpha* can be transported by live ducks (Johnson and Carlton 1996). In a preliminary experiment with live ducks, we noticed an intense predation on crayfish. Mallards (*Anas platyrhynchos*) are the most common duck species in Portugal and one of the most common species in the northern hemisphere. Actually, in

habitats such as rice fields that are shared by large numbers of mallards and *P. clarkii*, the latter constitute approximately 5 % of the volume of mallard food items and occur in 15 % of their stomachs (Rodrigues et al. 2002). The inclusion of crayfish in mallards' diet demonstrates that these two species share the same microhabitats and provides an indication that the transport is likely to occur. Moreover, other waterbird species are known to predate the introduced *P. clarkii*, which further enhances the probability of bird transport (Marques and Vicente 1999; Correia 2001; Lourenço 2010; Tablado et al. 2010).

Money, legislation, and effort have been applied with little success to the control of human activities that may spread *P. clarkii*. However, our findings support the idea that, once *P. clarkii* are introduced to one geographical region from a distant location, ectozoochory may allow them to reach habitats that would otherwise be inaccessible to autonomous dispersal. Therefore, we recommend that the possibility of waterfowl-mediated passive dispersal should not be discarded when managing invasions of the red swamp crayfish.

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