Evidence is provided for the first time that at least part of the egg bank of the southern African fairy shrimp Branchiopodopsis wolfi is dispersed over short distances by wind. A total of 423 sticky surfaces were mounted around and between individual basins at three rock pool sites, to trap any dispersing eggs during a 3 day period. Eight viable eggs were found in different egg traps (1.9% of the total), seven of which were located at one site with shallow basins. Given the proximity of vast egg banks to the egg traps, the low observed dispersal rate cautions against overestimating the importance of wind dispersal for population genetic processes. By generating egg banks to hedge against drought catastrophes, and producing egg types with different potential dispersibility, B. wolfi is a strong bet-hedger which has established a means of escaping temporal and spatial stress. These life history functions enable populations to persist in small desert rock-pools, which are the most extreme of temporary habitats.

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ADDITIONAL KEY WORDS:—resting eggs — egg banks — gene flow — metapopulations — risk-spreading.

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Anostracans are a conspicuous component of the biological communities of temporary aquatic habitats. The temporal and spatial variability of such (partially isolated) habitats is expected to favour selection for dispersal (McPeck & Holt, 1992; Gonzalez-Andujar, 1993) through the production of drought resistant resting eggs. The effectiveness of passive dispersal is demonstrated by their ability to colonize even remote oceanic islands (Brendonck, Thiery & Coomans, 1990; Peck, 1994), and by the broad distributions of some species (Banarescu, 1990; Hamer et al., 1994a,b). Wind (Riddoch, Mpoloka & Cantrell, 1994) and animal vectors (Brendonck, Thiery & Coomans, 1990; Saunders, Belk & Dufford, 1993) have been suggested as important dispersal agents, but few, if any, direct measurements have been made in relation to anostracans or any other zooplankton groups.

Despite their apparent dispersibility, significant genetic variation is generally observed among (often nearby) local populations of both asexually and sexually reproducing pond invertebrates, including anostracans (Hebert, 1974; Innes, 1991; Boileau, Hebert & Schwartz, 1992; Boileau & Taylor, 1994; Hebert & Wilson, 1994; Thier, 1994; De Meester, 1996; Davies, Simovich & Hathaway, 1997), while basins in the vicinity of inhabited pools of apparently equal quality are often empty (Bishop, 1967; Boileau & Hebert, 1991; Boileau & Taylor, 1994; Jenkins, 1995). Whether this is the product of limited dispersal or unsuccessful colonization/immigration is an issue of controversy (e.g. review in De Meester, 1996). There is also no clear relationship between dispersal inferred from local genetic divergence, and species distributions (Boileau & Hebert, 1988; Boileau, Hebert & Schwartz, 1992). It is therefore debatable whether these taxa are ‘adapted’ to disperse, or whether their dispersal ability is merely a consequence of their resistance to the harsh phase of their habitat.

Species of the anostracan genus *Branchipodopsis* are distributed widely in southern and eastern Africa (Barnard, 1929; Hamer & Appleton, 1996) and are the only anostracans in the region to persist in short-lived rock pools. Riddoch *et al.* (1994) found genetic evidence for isolation by distance between pools within a local metapopulation of *B. wolfi* Daday in south-eastern Botswana, and suggested that wind dispersal could have caused this pattern. We report on an attempt to directly confirm wind as an agent of dispersal in this species. The significance of these findings for the generation and maintenance of genetic divergence among neighbouring populations at three sites is discussed.

**MATERIAL AND METHODS**

*The species*

*Branchipodopsis wolfi* is the most widely distributed species of the genus, occurring in southern and eastern Africa, and displaying a high level of morphological
variability (Hamer & Appleton, 1996). It is characterized by rapid maturation (4–5 days) and high fecundity (daily broods of 30–150 resting eggs) (LB, unpublished data). Eggs are carried for less than a day in the ventral brood pouch before they are deposited. Broods are shed at once and eggs sink singly to the bottom. Hatching is light and temperature-dependent, and not all eggs hatch during a single inundation (Brendonck et al., 1998), generating egg (seed) banks that vary among pools and seasons between about 200 and 500 000 eggs per pool (1000 and 220 000 eggs m$^{-2}$, respectively) (LB & BR, unpublished data). All eggs have a shell with polygonal sculpturing; some are sticky and collect debris whereas others remain clean (Fig. 1).

Study sites

All three study sites are situated in south-eastern Botswana; two in the vicinity of Gaborone (Kgale Hill, KH and Kgale Siding, KS) and one about 50 km to the west (Thamaga, TH) (Fig. 2). Each location consists of a compact granite outcrop with several pool depressions of variable shape and depth, which are generally less than 10 m apart. During the wet season (October–April), pools fill intermittently and often dry prematurely. The average hydroperiod of individual pools ranges from 5 days to more than 1 month depending on the shape of the pools (maximum unknown due to yearly observation periods of only 1 month). Thamaga basins are more shallow (8.3 ± 3.0 cm, $n=13$) and with a lower incidence of aquatic vegetation (33% of pools) than those at KS (9.0 ± 2.6 cm deep, 53% of pools vegetated, $n=17$) and KH (12.6 ± 3.5 cm deep, 50% of pools vegetated, $n=4$). Thamaga pools also have a shorter mean observed hydroperiod (12 ± 3 days) than pools at the other sites (KS: 18 ± 8 days; KH: 23 ± 12 days).

Each site is characterized by spatial heterogeneity between pools and temporal heterogeneity within pools, in terms of population density, depth of water column, depth of sediment, nutrient status, presence/absence of vegetation, and turbidity. This may occur both in the course of a single inundation and between successive inundations. A single pool shows different probabilities of drying up between
inundations, depending on initial volume, recharge by subsequent rainfall events, and factors affecting evaporation rate. During the dry season, pools vary in the amount of sediment present, from vegetated pools with a thick organic layer, to unvegetated pools with only a thin, dusty covering.

**Data collection**

Egg traps were constructed in the form of cardboard quadrats (10 x 10 cm) that were covered on both sides with a self-adhesive plastic film. The top surface of these traps remained sticky for about 36 hours in the field. Most quadrats were mounted at approximately 1 metre intervals around selected pool margins to estimate the rate of outgoing, and to a lesser extent of incoming, eggs. The distance between traps and each egg bank varied with the depth of the pool basin and the horizontal distance between the margins of pools and sediment, but was usually between 10 and 50 cm. Some additional quadrats were mounted on the rocky surface between pools to trap so-called 'egg rains'. The orientation according to compass points was written on each quadrat with the intention of calculating the dominant direction of dispersal. A total number of 423 quadrats was used: 136 around 13 pools and 15 between pools at TH; 62 around 10 pools and 15 between pools at KS (repeated three times due to little wind); and 31 around 6 pools and 10 between pools at KH (Fig. 3). Each site was visited for two consecutive days to replace wind-blown quadrats. On the third day quadrats were transported to the laboratory where they were screened for the presence of viable eggs using a Wild M5 dissection microscope. Eggs were considered viable when the embryo popped out when squashed under water.

**RESULTS**

A total of eight viable eggs, two of which were of the sticky type, were trapped around four pool margins at TH and one at KH (Fig. 3). With the exception of
one pool at TH, all eggs were captured around unvegetated basins with little sediment. No quadrat contained more than one egg. No eggs were collected at the KS site or on any of the quadrats mounted between the pools that were aimed at capturing ‘egg rains’. Eggs at the TH site were dispersed in all directions but the sample size of successful traps was too small to calculate the average (dominant) direction of dispersal according to compass points.
This is the first time that wind-borne dispersal has been confirmed experimentally in pond-dwelling crustaceans. However, the low number of successful traps (1.9%), especially given the relatively large sample size (423 egg traps) and the proximity of traps to the generally extensive egg banks, cautions against overestimating the importance of wind as an agent of dispersal in Branchipodopsis wolfi. On the other hand, the sampling period of 3 days gives only a very momentary record. Future experiments will, therefore, aim at using traps with long-lasting glue to prolong the observation period during the generally very windy autumnal equinox (September).

With one exception, all eggs were trapped around pools at one rock pool site (TH). If this pattern prevails over the whole site, egg dispersal may enhance the persistence of this metapopulation in the heterogeneous environment (Hansson, 1991; Perry & Gonzalez-Andujar, 1993). Additional potential short-range vectors of B. wolfi resting eggs are overflow from one rock pool to another of floating eggs (all sites), cattle (TH), and waterfowl (due to the proximity of a dam at KS).

It is unclear whether the entire egg bank of B. wolfi is equally available for wind dispersal or if only the most recently produced (superficial) fraction is transferred. In non-vegetated pools, the amount of sediment is so small that it might reasonably be expected that the entire egg bank is subjected to wind action. Low observed dispersal rates at KS and KH, in comparison with the TH site, may arise from either physical reduction of wind dispersal (more vegetation, deeper basins) or the evolution of low dispersal rates out of locally adapted populations at the former two sites (McPeek & Holt, 1992). If pool depth and sediment stability significantly inhibit dispersal, we expect levels of localized gene flow to decrease as ponds age. This would make it very difficult to draw species-level inferences about gene flow and dispersibility.

Our findings do not prove that eggs are optimal propagules for wind dispersal, but do show that eggs can be dispersed by wind. It is unknown how morphological features of resting eggs relate to dispersal efficiency (Pajunen, 1986) but, in comparison to plant seeds, eggs of most anostracans, including B. wolfi, are relatively ‘unassisted’ (Oakwood et al., 1993; Hughes et al., 1994), lacking wings, plumes or hairs that increase air resistance. Eggs of several anostracan species resemble golf balls (Brendonck & Coomans, 1994a,b), which are designed for minimal wind resistance (Richard Hill, pers. comm.), suggesting effective wind dispersal once they get lifted. On the other hand, the surface-enlarging sculpturing of the egg shell has been suggested to inhibit dispersal by promoting adhesion of particles or attachment to the substrate (Brendonck et al., 1992; Brendonck & Coomans, 1994b).

Egg dispersal and gene flow

Significant levels of local genetic differentiation (reduced gene flow) at KS and KH, but not at TH (LB, BR & Luc De Meester, unpublished data) correspond with the present data that directly confirmed wind dispersal of eggs only at TH. Our findings also do not contest the hypothesis of Riddoch et al. (1994) that wind could be the most important agent of localized gene flow in semi-arid environments. Eggs
were, however, always trapped in low numbers and never more than 50 cm from
the egg banks. It remains therefore to be tested what the chances are that eggs
dispersing by repeated short jumps will land in appropriate sites, hatch and survive
to maturity. Other potential vectors such as overflow among pools could be more
important in causing gene flow, although this could not be confirmed from the
genetic pattern of KS populations by Riddoch et al. (1994).

On the other hand, gene flow can to some extent be uncoupled from dispersal
rate by low hatching of immigrant eggs, inter-pool heterogeneity of stresses (hard
selection), or competition with a locally adapted resident population (soft selection).
Patterns of genetic differentiation can therefore lead to underestimation of dispersal
rates and underlines the need of direct observations.

Egg dispersal and distribution

Like several other species with locally fragmented gene pools (see Boileau et al.,
1992; Boileau & Taylor, 1994), B. wolfi has a large distribution area (Hamer &
Appleton, 1996). This suggests that dispersal may be a more effective strategy for
colonizing new sites than for maintaining gene flow. Both colonization and im-
migration are probably slow processes, with dispersal only proceeding in short jumps.
In daphniids, estimated median dispersal distances of ephippia to invade unoccupied
rock pools from the closest source populations were between 5 and 9 m (Pajunen,
1986). Dominance of short-range dispersal in B. wolfi may have resulted in the large
morphological variability between regions (Hamer & Appleton, 1996), probably
resulting from prolonged geographic isolation. Longer range dispersal would be
maladaptive given the patchy distribution pattern of rock pool environments in a
matrix of unsuitable environment for establishment (Ellner & Shmida, 1981).
Belk (1974) even found morphological differences between anostracan rock pool
populations separated by less than 22 km. Conflicting views on dispersal rate in
zooplankton are reviewed in Maly & Bayly (1991) and De Meester (1996); these
reviews show the need for more direct assessments of dispersal abilities in zooplankton.

Risk-spreading

It may logically be inferred that the sticky eggs of B. wolfi, which are covered with
particles from the moment of their deposition (LB, pers. obs.), are less dispersal-
prone than the smooth ones (Fig. 1). Both types may therefore represent a dimorphic
dispersal strategy analogous to seeds (Venable & Levin, 1985) and insect wings
(Harrison, 1980; Roff, 1986). Such a mixed (risk-spreading) strategy often occurs
when carrying capacities vary spatially and temporally (Cohen, 1967; Gadgil, 1971;
McPeek & Holt, 1992). Future research will reveal if, similar to plants (Venable &
Lawlor, 1980; Venable & Brown, 1988), a trade-off exists between dispersal ability
and hatchability in both B. wolfi egg types.

The generation of multi-year egg banks and the production of egg types with
different dispersal potentials make B. wolfi an extreme bet-hedger with means to
respond to unpredictable habitat availability/suitability in both time and space. This
combination of life history attributes reduces the impact of environmental variation
at the expense of arithmetic-mean fitness (Venables & Brown, 1988) and allows B. \textit{wolff} to survive in the most extreme of temporary habitats: small desert rock-pools.

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