Odonatologica 16(3): 249-259 *September 1, 1987*

BREEDING SITE FIDELITY IN *PLATHEMIS LYDIA* (DRURY) (ANISOPTERA: LIBELLULIDAE)

W.D. KOENIG and S.S. ALBANO
Hastings Reservation and Museum of Vertebrate Zoology, University
of California, Star Route Box 80, Carmel Valley, California 93924,
United States

Received November 26, 1986 / Accepted January 4, 1987

Breeding site fidelity of adult *P. lydia* was studied at a small pond in central coastal California. Both males and females returned in equal proportions following marking. No morphological or behavioural differences were detected between males that dispersed and those not observed to disperse. Male dispersal occurred primarily soon after capture and among relatively old males that were at or near the end of their reproductive lifespan. These latter individuals often wandered widely, but only rarely obtained matings. Transplanted males disappeared more frequently after marking than individuals not transplanted; however, those observed again were as likely to remain at the pond to which they were transplanted as were marked, untransplanted residents. The results indicate that adult dispersal in this species during the reproductive period is small.

INTRODUCTION

Breeding site fidelity is an important life history trait. If individuals are faithful to the same site, gene flow will be constrained, facilitating population structuring and increasing the potential for evolutionary change. In addition, the same individuals will tend to interact within subpopulations, facilitating the evolution of social behaviours. Furthermore, studies of lifetime reproductive success are usually predicated on the assumption of negligible dispersal in the reproductive stage. Because such studies are relatively common in odonates (e.g., FINCKE, 1982, 1986, in press; BANKS & THOMPSON, 1985a; McVEY, in press; KOENIG & ALBANO, 1987), examination of breeding site fidelity is of general interest to those measuring or modelling selection in natural populations.

Here we describe breeding site fidelity in *Plathemis lydia* (Drury), and correlate site fidelity with body size, recent reproductive history, and behaviour. Dispersers were documented during brief daily observations at two ponds near the focal study pond. We also transplanted individuals caught at these nearby ponds to the main study pond, allowing us to document the degree to which breeding site fidelity was maintained in the face of displacements on the order of 0.6 to 1.2 km.

STUDY SITE AND GENERAL NOTES

Plathemis lydia is a medium-sized dragonfly widespread in North America. Breeding occurs on ponds and along slow moving creeks. Males defend small (≈ 10 m in length) territories for several hours each day, while females visit ponds for a few minutes at one to four day intervals solely for mating and oviposition (KOENIG & ALBANO, 1985). Neither sex feeds while at breeding ponds. Additional details on the life history and behaviour of this species can be found in JACOBS (1955), CAMPANELLA & WOLF (1974), McMILLAN (1984), and KOENIG & ALBANO (1985).

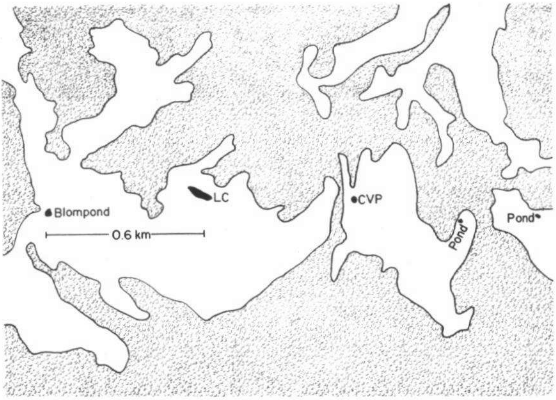

Fig. 1. Map of the study area, located adjacent to Hastings Reservation in central coastal California, USA. Savannas are depicted by open areas; forested areas are oak woodland and chaparral. Marked are Blompond, where observations were continuous, Laguna Conejo (LC) and Corral Viejo Pond (CVP), where we checked for dispersers, and the next two ponds closest to the study site. These latter 4 ponds are 0.6, 1.2, 1.7, and 2.1 km from Blompond, respectively, and were the only breeding localities within 3 km of Blompond during the study period. All ponds are between 500 and 550 m in elevation.

The study was conducted during summer 1984 on land adjacent to Hastings Reservation, approximately 30 km inland in central coastal California. The primary study site was Blompond, a small seasonal stock pond approximately 380 m² in area. As part of a study of the behavioural ecology of *P. lydia*, all males breeding at Blompond and as many females as possible were captured. For each individual we measured hind wing length, the condition of its wings (on a scale of 1 to 3 where 1 = fresh, 2 = moderately worn, and 3 = very worn), and marked their wings and abdomen with small dots of enamel paint for individual recognition. Beginning on 19 June and extending until breeding activity ended on 5 August, we maintained continuous surveillance at the pond during all hours dragonflies were present. We recorded all breeding activity of *P. lydia* and recorded all males present at 20 min intervals. Additional details of our field procedures are described in KOENIG & ALBANO (1987)

Once or twice daily we made brief (≈ 15 min) visits searching for marked individuals at each of the two nearest breeding sites. The nearer, Laguna Conejo (LC), is a natural vernal pond up to 1200 m² in size located 0.6 km NW of Blompond. The farther, Corral Viejo Pond (CVP), is a stock pond approximately 300 m² in area located along a straight line with Blompond and LC and 1.2 km away from the former. All three ponds are at about the same elevation (510 m) and are separated by oak woodland and savanna. The next two breeding sites for *P. lydia* are another 0.5 and 0.9 km beyond CVP. A map of the study area is presented in Figure 1.

In order to investigate breeding site fidelity among displaced individuals, we captured individuals at LC and CVP and transplanted them to Blompond, where they were released within 2 hours. The prior histories of these individuals were not known.

RESULTS

SITE FIDELITY FOLLOWING MARKING

A total of 91 males and 31 females were marked at Blompond on or after 19 June; in addition, 57 males and 9 females were transplanted to Blompond from either LC or CVP (all but 7 from the latter). The number and proportion of these individuals observed after marking are summarized in Table I. Of residents marked and released at Blompond, 75% of males and 74% of females were seen again. Table I also lists the number of residents and transplants first seen after marking at each of the three focal ponds. None of the females was ever observed at either LC or CVP, while 10 males (11% of all those marked or 15% of all those resighted following capture) were first seen following marking at either LC or CVP. The mean number of days between marking and the subsequent first resighting was 1.09 days for males returning to Blompond and 4.20 days for those dispersing to LC or CVP, a significant difference.

Among male transplants, only 42% were resighted, a proportion significantly lower than among male residents caught and released at Blompond ($\chi^2 = 14.5$, df $= 1$, $P < 0.001$). The proportion of female transplants resighted following capture was 44%, very similar to that for males. However, this value is not significantly different from the 74% of resident females resighted ($\chi^2 = 1.6$, df $= 1$, ns).

Although male transplants were less likely than residents to be resighted, among those seen again following marking there was no difference in the proportion returning immediately to Blompond (85% of resighted residents versus 75% of resighted transplants; $\chi^2 = 0.7$, df $= 1$, ns) compared to those dispersing to LC or CVP. Among both residents and transplants, the majority of dispersers were seen at the nearer LC. Male transplants returning to Blompond were first observed an average of 2.11 days following marking, significantly longer than the time between marking and subsequent first resighting for residents returning to Blompond (Mann-Whitney U test, $z = 2.2$, $P < 0.05$), but significantly less than the number of days between marking and subsequent first resighting for transplants dispersing to either LC or CVP ($z = 2.9$, $P < 0.01$; Tab I). There was no difference in the number of days between marking and first resighting among resident and transplant females returning to Blompond, but the sample of transplants is small.

In summary, significantly fewer transplants were observed following marking than residents, but the same proportion of resighted transplants and residents

Table I

Breeding site fidelity of *Plathemis lydia* marked at and transplanted as adults to Blompond

	Males	Females	Total
Marked at Blompond			
Total marked	91 (100%)	31 (100%)	122 (100%)
Not seen again	23 (25%)	8 (26%)	31 (25%)
Seen again	68 (75%)	23 (74%)	91 (75%)
Blompond (BP)	58 (64%)	23 (74%)	81 (66%)
Laguna Conejo (LC)	8 (9%)	—	—
Coral Viejo Pond (CVP)	2 (2%)	—	—
Days between marking and first subsequent observation for those			
Returning to Blompond	1.09±1.06 (58)	1.43±0.95 (23)	1.19±1.04
	***		
Dispersing to LC or CVP	4.20±2.57 (10)	—	—
Transplanted to Blompond from LC or CVP			
Total marked	57 (100%)	9 (100%)	66 (100%)
Not seen again	33 (58%)	5 (56%)	38 (58%)
Seen again	24 (42%)	4 (44%)	28 (42%)
Blompond (BP)	18 (32%)	4 (44%)	22 (33%)
Laguna Conejo (LC)	4 (7%)	—	—
Corral Viejo Pond (CVP)	2 (4%)	—	—
Days between marking and first subsequent observation for those			
Returning to Blompond	2.11±2.45 (18)	1.50±1.00 (4)	2.00±2.25 (22)
	**		
Dispersing to LC or CVP	4.17±1.33 (6)	—	—

Tests by Mann-Whitney U: ** $P < 0.01$, *** $P < 0.001$. Data are x ± SD (n)

remained at Blompond as dispersed to LC or CVP. Resident males that stayed at Blompond returned significantly sooner following marking than resident males that dispersed or transplant males that stayed at Blompond following release.

CHARACTERISTICS OF DISPERSERS

The site fidelity of adult *P. lydia* residents caught at Blompond and subsequently seen again is summarized in Table II. None of the 23 females in this category was ever observed at either LC or CVP. However, this apparent lack of dispersal among females is probably an artifact: the briefness of both the visits made by females to ponds (KOENIG & ALBANO, 1985) and of our own surveys rendered the detection of marked females visiting LC or CVP unlikely. Consequently, our information on dispersers comes exclusively from males.

Of the 59 male residents observed after capture, 71% were observed only at Blompond during their lives, 19% were seen at LC at least once, and 14% were seen at CVP at least once during their lives (two individuals were observed at both

Table II

Characteristics of site-faithful and dispersing *Plathemis lydia* adults

	Males	Females	Total
N observed after marking	59 (100%)	23 (100%)	82 (100%)
N never observed at LC or CVP	42 (71%)	23 (100%)	65 (79%)
N observed at LC	11 (19%)	0 (0%)	11 (13%)
N observed at CVP	8 (14%)	0 (0%)	8 (10%)
N returning to BP after being observed at LC or CVP	3 (5%)	—	—
Mean days between first and last observation at Blompond before dispersal or disappearance			
Those never seen elsewhere	6.52±7.60 (42)	4.35±5.04 (23)	5.75±6.85 (65)
	(ns)		
Those observed at LC or CVP	5.35±6.79 (17)	—	—
Mean hind wing length			
Those never seen elsewhere	31.7±0.80 (41)	33.0±0.90 (22)	—
	(ns)		
Those observed at LC or CVP	31.6±0.53 (16)	—	—
Mean wingwear category			
Those never seen elsewhere	1.9±1.0 (14)	1.3*±0.6 (19)	—
	(ns)		
Those observed at LC or CVP	2.0±0.8 (4)	—	—
Mean lifetime number of matings			
Those never seen elsewhere	13.7±23.8 (42)	2.7±1.8 (23)	—
	(ns)		
Those observed at LC or CVP	7.6±11.5 (17)	—	—

Tests by Mann-Whitney U: ns = $P > 0.05$. Data are x ± SD (n)

LC and CVP). Three males (18% of the 17 individuals that dispersed) returned to Blompond for at least one 20 min census after having dispersed to either LC or CVP.

Table II also compares several characteristics of "non-dispersing" males — those marked and returning to Blompond that were never observed elsewhere — with "dispersing" males that were subsequently observed at either LC or CVP at least once. No significant differences were found between the males in these two categories for the number of days they remained at Blompond prior to disappearance (for non-dispersers) or dispersal, mean hind wing length, the degree of wingwear when marked, or total number of matings achieved at Blompond. Thus, there appears to be no obvious morphological or behavioural difference between known dispersers and those which were never observed at either of the two nearest ponds.

Table III

Mating success and time spent breeding for site-faithful and dispersing *Plathemis lydia* males present at Blompond for two or more days

	Dispersed (*n=11*)	Did not disperse (*n=31*)	z-value
Matings the day prior to dispersal or disappearance	0.18±0.41	0.48±0.81	1.1
Mean number of matings all days present at Blompond	1.21±0.82	1.25±1.25	0.4
z-value	3.2**	3.0**	
Hours at Blompond the day prior to dispersal or disappearance	0.97±0.77	1.99±1.43	2.3*
Mean hours present all days at Blompond	2.41±1.31	2.52±1.16	0.3
z-value	2.7*	1.9	

Tests by Mann-Whitney U: * $P < 0.05$, ** $P < 0.01$. Data shown are $\bar{x} \pm SD$

Additional comparison of male dispersers with non-dispersers is presented in Table III. Included in this table are only males caught and released at Blompond that were observed there on at least two days subsequent to capture. Again there were no differences in the number of matings achieved by males in the two categories the day prior to dispersal or disappearance, or in the mean number of matings achieved during all days they were at Blompond. However, for both dispersers and non-dispersers, the number of matings achieved on their final day at Blompond was significantly less than the average number of matings they obtained during all days they had been present at Blompond.

There was also no difference in the mean number of hours dispersers and non-dispersers spent at Blompond during the days they were present. Dispersers, however, spent significantly less time at Blompond on the day immediately prior to dispersal than did individuals that disappeared. There was also a significant decrease in the time spent by dispersers, but not non-dispersers, the day prior to dispersal or disappearance compared to the mean number of hours spent at Blompond all days they were present.

DISCUSSION

Approximately 25% of *P. lydia* disappear permanently following capture and marking (Tab. I). This value is a combination of natural mortality, mortality induced by handling, and long-distance dispersal beyond the two nearest ponds (LC and CVP). Of all male residents, 11% dispersed to one of the two nearest ponds immediately following capture. No dispersing females were found, but this difference may be primarily the result of our sampling procedure and sexual differences in reproductive patterns. Males are territorial and may remain on a breeding pond for up to several hours each day, while females visit ponds for only a few minutes every several days to mate and oviposit (KOENIG & ALBANO, 1985). Thus, we were far less likely to observe marked females at either LC or CVP than marked males. Our procedure also did not allow us to find individuals, either males or females, casually visiting the two dispersal ponds. However, we are likely to have seen a majority of males settling at LC or CVP and remaining there for more than a short time on a single day.

Individuals transplanted to Blompond from LC and CVP were less likely to be seen again than residents that were marked and not transplanted, significantly so for males. Transplants that stayed at Blompond also took significantly longer to return than did residents. However, of transplants seen following marking, the proportion remaining at Blompond compared to returning to LC or CVP was the same as among residents. Transplants may be more vulnerable than residents to predation or long-distance dispersal, possibly because of the longer period we handled them during marking (the time from capture to release was up to 2 hours for transplants and involved keeping them in coolers, while residents were usually marked and released within 5 min). Otherwise, transplants and residents had similar breeding site fidelity. Indeed, several of the transplants remained at Blompond and were reproductively quite successful. ♂ 6014, for example, was transplanted from CV pond on 8 July. Between 11 July and 19 July he was present at Blompond every day and obtained 23 matings, making him one of the most successful males during the study. Eleven other males (19% of all transplants) were present at Blompond on two or more days following release.

We compared resident males eventually observed at either LC or CVP with those never observed anywhere besides Blompond, and found that both groups remained at Blompond for a similar length of time before dispersal, had similar hind wing length, and wings in similar condition when marked (Tab II). Males that dispersed had lower mating success than those never observed elsewhere, but the difference is not significant. Thus, there appear to be no obvious behavioural or morphological characters distinguishing males that eventually dispersed from those that were never seen at either LC or CVP.

The conclusion that dispersers and non-dispersers do not differ in their reproductive success is further supported by the lack of any difference between either their average daily mating success or the number of matings obtained on their last day at Blompond (Tab. III). Both dispersers and non-dispersers obtained fewer matings on their last day at Blompond than they averaged during all days they were present at the pond. Dispersers were also present at Blompond for a significantly shorter period of time on their last day than they had averaged during all days they were present, or than were non-dispersers the day before they disappeared. Because the duration of territorial behaviour of *P. lydia* at the densities observed in 1984 appears to be energetically constrained (KOENIG & ALBANO, 1985), this latter finding suggests that individuals may disperse following a period of energy stress such as might result from poor foraging success.

What prompted individuals to disperse? The relatively high proportion of individuals dispersing immediately following marking (Tab. I; cf. also KOENIG & ALBANO, 1985) suggests that the trauma involved with capture and marking may have induced dispersal. However, because all resident males were marked, those caught at Blompond were known to have recently dispersed there. Thus, these males had not yet settled and may have been in the midst of a search for a breeding site. Such long-distance dispersal may lead to the colonization of new breeding sites (e.g. MOORE, 1954).

Males that returned to Blompond following marking also frequently dispersed later on: of 59 males seen first at Blompond after release, 17 (29%) eventually dispersed to either LC, CVP, or both (Tab. II). Of these 17, only 3 (18%) were ever seen again at Blompond, and all of these were seen only once. Thus, these latter dispersal events were generally irreversible.

Further examination of the 17 males that stayed at Blompond following marking but later dispersed suggests two primary patterns (Fig. 2). Over a third (35%) returned to Blompond for only one day following marking and then dispersed; four of these males were only observed at Blompond for a single 20 min census, while one each was present during two and three censuses. Thus, these individuals moved soon after capture and probably did so at least in part because of handling.

Eight individuals (47% of the dispersers) returned to Blompond following marking and remained there for 5 to 18 days, after which they dispersed to LC or CVP. Although our data following dispersal are limited, we propose that these individuals were engaging in post-reproductive wandering. Several lines of evidence are consistent with this hypothesis.

First, as shown in Table III, on the day prior to dispersal the mating success of dispersing individuals was very low (0.18 matings/individual) and the mean time they spent at Blompond was very short (< 1 hr). Since dispersers were not significantly less successful overall than non-dispersers (Tables II, III), this indicates that these individuals were experiencing particularly poor success just prior to emigrating.

Second, individuals that dispersed following five or more days at Blompond were usually not observed repeatedly at either of the other two ponds we checked, suggesting that they either continued to wander or did not survive long following dispersal. Of the eight individuals present at Blompond for five or more days and then dispersing, two were observed at LC on one day only; one of these later returned to Blompond for a single census before disappearing entirely. Three others were observed at LC on two separate days prior to disappearance. Another two were observed once each at both LC and CV prior to disappearance. Only one was observed repeatedly at the pond to which he dispersed.

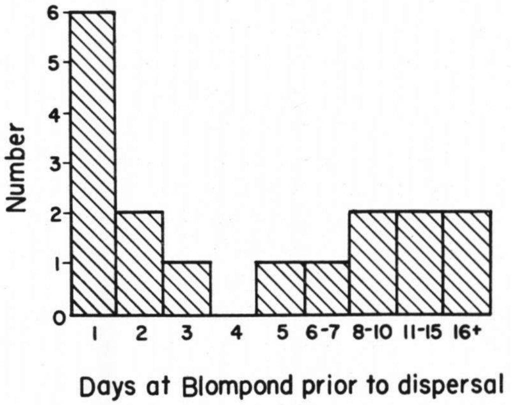

Fig. 2. The number of days dispersing male *P. lydia* remained at Blompond prior to dispersing to either LC or CVP. Included are males that were marked at and subsequently seen at Blompond at least once. The maximum length of time a male remained prior to dispersal was 18 days. N = 17.

Third, none of the three males that were seen at Blompond after dispersing to either LC or CVP were ever territorial or obtained any matings during their brief return to Blompond. Although we do not have breeding information on these individuals while present elsewhere, these data suggest that these males were unsuccessful at obtaining matings and were spending only a short time at potential breeding localities.

Fourth, during the course of the study we marked 15 males at Blompond whose wings were quite worn (wingwear = 3) and thus had most likely been reproductive for at least several days. Because all resident males were marked, these males must have lived elsewhere prior to dispersal to Blompond. Of these 15 males, six were not seen again following marking, two were seen again at LC only, four were observed at Blompond only one day subsequent to capture, and the remaining three were seen at Blompond on 2 to 4 days following capture.

Only one (7%) obtained any matings at all at Blompond, and that male, one of the three that remained at Blompond for several days following capture, only obtained a single mating. These data suggest that, as with residents we observed dispersing to LC and CVP following reproduction at Blompond, the males with worn wings we caught at Blompond were wandering at the end of their reproductive careers. Gene flow resulting from such wandering is minimal.

Most prior work on dispersal in odonates has focused on zygopterans, and has generally shown breeding-site fidelity to be strong (MITCHELL, 1962; UEDA, 1976; BANKS & THOMPSON, 1985b). In a study of *Lestes barbarus* involving transplants, UTZERI et al. (1984), demonstrated strong natal philopatry, relatively little dispersal by adults, and lower returns of displaced individuals to the pond at which they were caught than controls.

Among Anisoptera, MOORE (1954) categorized several distinct types of dispersal including emergence flights, wandering in both the immature and adult stages, and mass migration. Some of these dispersal types involve considerable distances, as evidenced by colonization of ponds many kilometers away from other breeding sites. In *Pyrrhosoma nymphula,* CORBET (1952) found that older individuals may leave breeding ponds when relatively high densities of newly matured individuals arrive. This may lead to wandering in the adult stage (MOORE, 1954) similar to that which we described here.

We do not have data on natal philopatry in *P. lydia.* However, little emergence took place at Blompond and we thus suspect that the population was largely made up of emigrants from elsewhere. Pre-reproductive adults undergo a period of wandering in search of a suitable pond to breed. Such individuals may be easily induced to disperse elsewhere, as indicated by the 10 males that dispersed to LC or CVP immediately following capture and the six others that returned to Blompond for only a short time on a single day following capture and then dispersed.

Dispersal is minimal during the period that males are actively breeding. Even transplants, many of which are likely to have been breeders at LC or CVP prior to displacement, often remained at Blompond following marking, suggesting that homing is not strong and that breeders tend to remain at whatever pond they find themselves as long as they are capable of breeding.

Our results indicate that gene flow among sub-populations of *P. lydia* is primarily the result of dispersal by pre-reproductives. Subsequent dispersal occurs, but usually involves only post-reproductive individuals. Thus, it is acceptable to ignore dispersal during the reproductive stage when considering lifetime reproductive success in this species (e.g. KOENIG & ALBANO, 1987).

ACKNOWLEDGMENTS

We thank A. PETERS & M. PETERSON for field assistance, R. NOYCE for access to the study

site, and K. HECK for comments on the manuscript.

REFERENCES

BANKS, M.J. & D.J. THOMPSON, 1985a. Lifetime mating success in the damselfly, Coenagrion puella. *Anim. Behav.* 33: 1175-1183.

BANKS, M.J. & D.J. THOMPSON, 1985b. Emergence, longevity and breeding area fidelity in Coenagrion puella (L.) (Zygoptera: Coenagrionidae). *Odonatologica* 14: 279-286.

CAMPANELLA, P.J. & L.L. WOLF, 1974. Temporal leks as a mating system in a temperate zone dragonfly (Odonata: Anisoptera). I: Plathemis lydia (Drury). *Behaviour* 51: 49-87.

CORBET, P.S., 1952. An adult population study of Pyrrhosoma nymphula (Sulzer): (Odonata: Coenagrionidae). *J. Anim. Ecol.* 21: 206-222.

FINCKE, O.M., 1982. Lifetime mating success in a natural population of the damselfly, Enallagma hageni (Walsh) (Odonata: Coenagrionidae). *Behav. Ecol. Sociobiol.* 10: 293-302.

FINCKE, O.M., 1986. Lifetime reproductive success and the opportunity for selection in a non-territorial damselfly (Odonata: Coenagrionidae). *Evolution* 40: 791-803.

FINCKE, O.M., in press. Sources of variation in lifetime reproductive success in a non-territorial damselfly (Odonata: Coenagrionidae). *In:* T.H. Clutton-Brock, [Ed], Reproductive success. Univ. Chicago Press, Chicago.

JACOBS, M.E., 1955. Studies on sexual selection and territorialism in dragonflies. *Ecology* 36: 566-586..

KOENIG, W.D. & S.S. ALBANO, 1985. Patterns of territoriality and mating success in the white-tailed skimmer Plathemis lydia (Odonata: Anisoptera). *Am. Midl. Nat.* 114: 1-12.

KOENIG, W.D. & S.S. ALBANO, 1987. Lifetime reproductive success, selection, and the opportunity for selection in the white-tailed skimmer Plathemis lydia (Odonata: Libellulidae). *Evolution* 41: 22-36.

McMILLAN, V., 1984. Dragonfly monopoly. *Nat. Hist.* 93(7): 32-39.

McVEY, M.E., in press. The opportunity for sexual selection in a territorial dragonfly Erythemis simplicicollis. *In:* T.H. Clutton-Brock, [Ed], Reproductive success. Univ. Chicago Press, Chicago.

MITCHELL, R., 1962. Storm-induced dispersal in the damselfly Ischnura verticalis (Say). *Am. Midl. Nat.* 82: 359-366.

MOORE, N.W., 1954. On the dispersal of Odonata. *Proc. Bristol Nat. Soc.* 28: 407-417.

UEDA, T., 1976. The breeding population of the damselfly, Cercion calamorum Ris. I. Daily movements and spatial structure. *Physiol. Ecol. Jpn* 17: 303-312.

UTZERI, C., G. CARCHINI, E. FALCHETTI & C. BELFIORE, 1984. Philopatry, homing and dispersal in Lestes barbarus (Fabricius) (Zygoptera: Lestidae). *Odonatologica* 13: 573-584.