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*Biol. Lett.* 2006 **2**, 325-329
doi: 10.1098/rsbl.2006.0487

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*Biol. Lett.* (2006) **2**, 325–329
doi:10.1098/rsbl.2006.0487
*Published online* 9 May 2006

# Simple rules guide dragonfly migration

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**Every year billions of butterflies, dragonflies, moths and other insects migrate across continents, and considerable progress has been made in understanding population-level migratory phenomena. However, little is known about destinations and strategies of individual insects. We attached miniaturized radio transmitters (*ca* 300 mg) to the thoraxes of 14 individual dragonflies (common green darners, *Anax junius*) and followed them during their autumn migration for up to 12 days, using receiver-equipped Cessna airplanes and ground teams. Green darners exhibited distinct stopover and migration days. On average, they migrated every 2.9±0.3 days, and their average net advance was 58±11 km in 6.1±0.9 days (11.9±2.8 km d$^{-1}$) in a generally southward direction (186±52°). They migrated exclusively during the daytime, when wind speeds were less than 25 km h$^{-1}$, regardless of wind direction, but only after two nights of successively lower temperatures (decrease of 2.1±0.6 °C in minimum temperature). The migratory patterns and apparent decision rules of green darners are strikingly similar to those proposed for songbirds, and may represent a general migration strategy for long-distance migration of organisms with high self-propelled flight speeds.**

**Keywords:** dispersal; insect; decision rules; flight; radiotracking

## 1. INTRODUCTION

The occurrence of insect migration is well known from behavioural observations (Williams 1957; Johnson 1969; Walker & Littell 1994) going back to biblical times (Childs 1974), and from radar and mark–recapture studies (Reynolds & Riley 2002). Major progress has been made in understanding butterfly (Malcolm 1987) and moth migrations on the population level, such as in the oriental armyworm (*Mythimna separata*; Chen *et al.* 1989), the rice leafroller (*Cnaphalocrocis medinalis*; Riley *et al.* 1995) or the black cutworm (*Agrotis ipsilon*; Showers 1997). Dragonfly migration occurs on all continents except Antarctica, and is also a well-documented phenomenon (Russell *et al.* 1998; Corbet 1999; Moskowitz *et al.* 2001; Freeland *et al.* 2003; Artiss 2004). Atleast 25 to 50 of the approximately 5200 dragonfly species worldwide are thought to be migratory (Russell *et al.* 1998). Approximately nine dragonfly species are common long-distance migrants in North America, flying annually north and south throughout much of the North American continent (Macy 1949; Turner 1965; Opler 1971; Arnaud 1972; Russell *et al.* 1998; Moskowitz *et al.* 2001; Sprandel 2001). Migrating Green Darners have even been recorded in the Gulf of Mexico on oil platforms (Russell 2005). Densities of migrating dragonflies sometimes rival those of locust swarms, with nearest neighbour distances of 3.1 m (Kormondy 1961).

Qualitatively, dragonfly migrations may appear remarkably similar to songbird migrations (Berthold 1993). Observations of apparently migratory dragonflies in the Northern Hemisphere peak in spring from March to early June (generally moving northward) and in autumn from August to October (generally moving southward; Freeland *et al.* 2003). The largest aggregations of dragonflies are seen along topographic leading lines, such as lake or seashores, cliffs, or ridges. Well-known examples are the coasts of Florida, shores of several of the Great Lakes, the Oregon and California coast, and the Atlantic coast and Delaware Bay at Cape May, NJ (Moskowitz *et al.* 2001). Large numbers of migrating dragonflies are recorded following the passage of cold fronts (Drake & Farrow 1988; Moskowitz *et al.* 2001). Dragonflies apparently prepare for migration by accumulating fat (Russell *et al.* 1998), as in songbirds (Berthold 1993) and other migratory insects (Williams 1957).

We tested for the first time whether there is a congruence of individual migration tactics between birds and dragonflies, such as distinct stopover and migration periods and/or dependence of individual migratory decisions on specific weather patterns (Cochran & Wikelski 2005).

## 2. MATERIAL AND METHODS

We captured 14 green darners (seven males, seven females) between 14 September and 30 October 2005 at five sites (salt marshes, old-fields, coastal dunes) in New Jersey, USA (38°55′–40°26′ N latitude). All were relatively newly emerged adults, as judged by the general lack of wing damage (figure 1*b*). Within 2 hours of capture, we sexed them and attached small (*ca* 300 mg) radio transmitters (Sparrow Systems, Fisher, IL, 2 radio pulses per second) to the ventral thorax using minute amounts of a combination of eyelash adhesive (Andrea glue, American International Industries, Commerce, CA) and superglue (Krazy Glue, Elmers, OH). One person held the dragonfly upside down with the wings held together above the thorax while another person attached the transmitter (figure 1*a*). Three darners were weighed (mean 1.2 g±0.3 s.d.) prior to transmitter attachment. Depending on ambient conditions, darners took off either immediately or within 3 minutes of release, and they flew away without apparent problems (see electronic supplementary material). We were unable to test whether the transmitter load affected flight performance, but we could not detect flight differences between tagged and untagged individuals during rapid foraging manoeuvres. Because dragonflies mate on the wing, with the male often carrying the female during copulation, and because dragonflies are known to capture and transport prey larger than their own weight (Wakeling & Ellington 1997; Taylor 2001), their ability to carry a 300 mg radio transmitter with little apparent difficulty is not surprising.

Once airborne, dragonflies were tracked from the ground using conventional radio telemetry techniques, such as tracking vehicles and handheld devices (Wikelski *et al.* 2003; Cochran *et al.* 2004). In addition, we located individuals at least twice a day using aerial surveys conducted from a Cessna 152 or 172 airplane equipped with external receiver antennas, weather permitting. We stopped

The electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2006.0487 or via http://www.journals.royalsoc.ac.uk.

*Received* 23 February 2006
*Accepted* 10 April 2006

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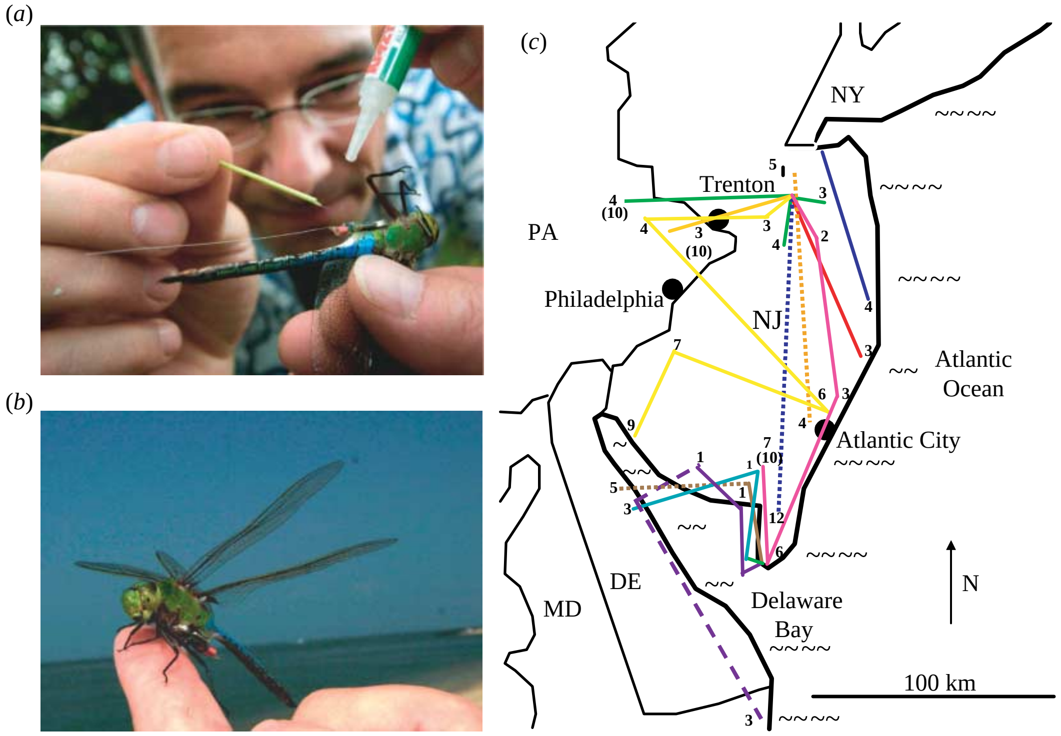

Figure 1. Attachment of radio transmitters and migration patterns during autumn migration in green darners. (*a*) Attachment of a 300 mg radio transmitter to the thorax of a green darner. (*b*) A green darner with transmitter shortly before take-off at Cape May Point (dark blue line at bottom of figure (*c*)) This individual shows the typically minor wing wear seen during our study, indicative of relatively recently emerged individuals. (*c*) Trajectories of migrating green darners along the northeastern seaboard of the USA (New York (NY) to Maryland (MD)). Different colours indicate different individuals, numbers depict days since tagging, numbers in brackets show maximum number of days individuals were tracked. Dotted lines indicate that it was unclear on which day individuals conducted their migratory flight. The dashed blue line indicates the most likely route of crossing Delaware bay. Shore lines are depicted by a thick black line, ocean by undulating lines. Pictures by Christian Ziegler.

surveying individual migration movements once dragonflies had moved out of our driving or flight range (above 140 km straight line from Princeton University, 40°20′ N, 74°40′ W) or after *ca* 10 days of transmitter life. We recorded no predation of tagged individuals, but we cannot eliminate the possibility that some of our missing transmitters were the result of mortality. However, we doubt that the predators of migrating green darners (Moskowitz *et al.* 2001)—mainly American kestrel (*Falco sparverius*) and merlin (*Falco columbarius*)—would destroy a radio transmitter to the extent that we could no longer find it. We observed kestrels separate the bodies of captured dragonflies from the wings and would expect the same for a radio transmitter.

We found no detectable differences in migration patterns between the sexes ($p > 0.3$ for all tests), and therefore lumped all data for final analysis. We used local wind and temperature information as collected every hour at the closest (max. distance *ca* 30 km) National Oceanic & Atmospheric Administration (NOAA) automated airport surface weather stations. For statistical analyses, we treated each individual as an independent data point and calculated average values for its migratory characteristics, such as the number of stopover days, days to first migratory flight or distance per migratory flight. Subsequently, we used individual averages ($n = 14$) for overall comparisons. For calculating stopover data and weather dependence of flights, we included data only for individuals whose locations were positively identified daily ($n = 11$). For two individuals, we report only total migration direction and distance because we did not know when they migrated. The last individual we tagged was tracked for 3 days, during which time it did not move far from the point of capture. We lost (and never re-found) its transmitter signal after day 3, presumably because that dragonfly migrated. In all analyses, we report population means ± s.e. (or mean vector ± circular s.d.). We used SPSS for WINDOWS v. 12.0 for all calculations except for circular statistics, for which we used ORIANA v. 2.02.

## 3. RESULTS

All captured individuals were recently emerged, judged by lack of wing wear (figure 1*a*,*b*). Even so most appeared sexually mature and some females were gravid. We followed individuals for an average of 6.1 ± 0.9 days. All individuals migrated during the time period we observed them (figures 1*c* and 2*a*), i.e. moved more than one day range (above 2 km radius; figure 2*b*) from the location of capture. Individuals initiated migration either on the day of capture ($n = 3$) or up to 4 days later ($n = 10$). On average, individuals migrated every 2.9 ± 0.3 days. Daily movement ranges exhibited a trimodal distribution: short range and omnidirectional (1–4 km), medium range and directional (8–12 km), or long range and directional (25–150 km; figure 2*b*). The average net advance of 13 migrating individuals was 58 ± 11 km (11.9 ± 2.8 km $d^{-1}$), and the average direction was towards 186 ± 52° (figure 2*a*).

Surface wind speeds on days when individuals migrated tended to be lower (13 ± 1.4 km $h^{-1}$) than on days when they did not migrate (18 ± 2.1 km $h^{-1}$; *T*-test, $t = 1.95$, $p = 0.063$). No dragonfly migrated when winds gusted above 25 km $h^{-1}$. Winds on days when green darners migrated were, on average, more northerly (37 ± 94°) than on non-migratory days (271 ± 58°; Watson–Williams, $F = 10.96$, $p = 0.003$). We found no differences in the daily high temperatures between flying days (24.3 ± 0.8 °C) and non-flying days (22.1 ± 1.5 °C; *T*-test, $t = 1.16$, $p = 0.25$). However, a flying day always succeeded a night that was colder than the previous night (average nocturnal temperature decrease 2.1 ± 0.6 °C), whereas non-flying

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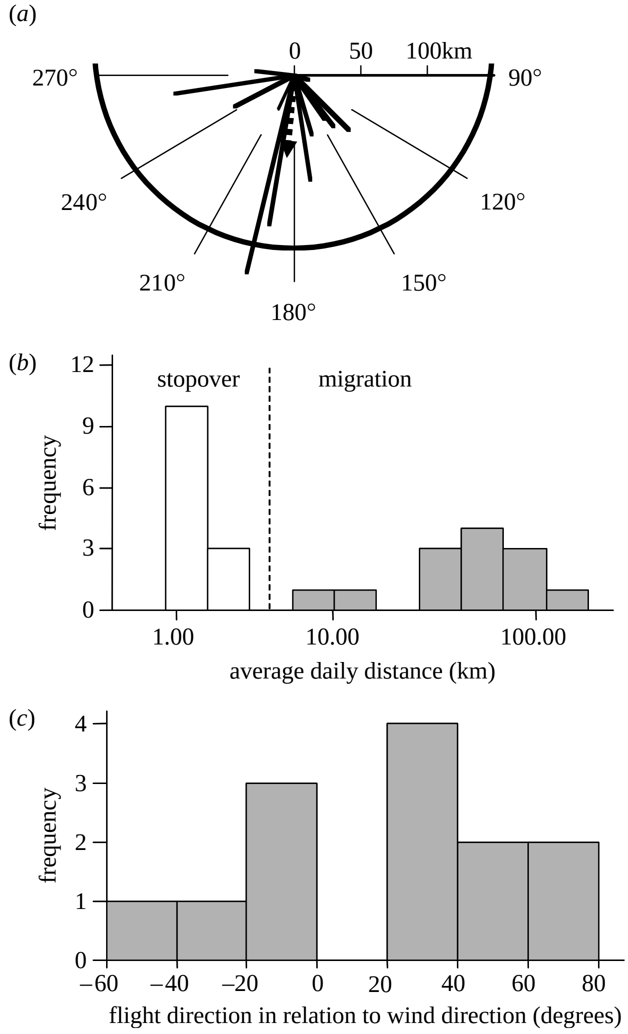

Figure 2. Migratory pattern in green darners during autumn migration. (*a*) Overall migratory advances of green darners during our study (black lines show individual migratory vectors). The dashed arrow depicts the average advance and direction of our study population. (*b*) Frequency histogram showing average migratory distances of 13 of 14 tagged green darners separated into stopover days (less than 4 km directional movement, white bars, one individual was not observed migrating) and migration days (grey bars). (*c*) Frequency histogram showing average flight direction of individual green darners in relation to wind direction (determined as surface wind at the midpoint of their migration flight).

days had on average warmer nights leading up to them (average temperature increase of 2.4±0.8 °C; *T*-test, $t=4.7$, $p<0.0001$, comparing two successive nights). Green darners did not seem to compensate strongly for wind drift (figure 2*c*), as their individual migration paths only differed by 20±11° from wind direction. Such behavioural rules often resulted in zig-zagging of flight paths on consecutive days (figure 1*c*).

Four green darners changed their migration route when hitting an ocean barrier (e.g. the 19 km wide Delaware Bay at Cape May Point, NJ, or the Atlantic shoreline). Two individuals (green and blue lines starting north of Delaware Bay in figure 1*c*) were recorded flying out over the ocean in a southerly or westerly direction for *ca* 5 km (as determined from signal strength pattern from the ground and from an airplane); they then reversed their flight direction and headed north. Both re-orienting individuals were subsequently found southwestward in the states of Delaware and Maryland, after having crossed the Delaware River. For the blue individual, we include an estimate of the most likely site of the river crossing (dashed line). The third individual (brown line, figure 1*c*) was only heading out over the ocean for *ca* 200 m and then migrated north before flying westward 4 days later. The fourth individual (pink line, figure 1*c*) stopped over in Cape May before heading north, where we abandoned it after 10 days of tracking.

## 4. DISCUSSION

Radio telemetry of individual dragonflies revealed astounding similarities between songbird (Berthold 1993) and large-insect migration (Williams 1957; Johnson 1969). Like songbirds, green darners showed distinctive stopover and migration days; they did not migrate during very windy days; and they migrated only when nocturnal temperatures decreased (cf. Cochran & Wikelski 2005). The reorientation behaviour of green darners upon reaching the tip of Cape May Point, NJ, mirrors that of numerous songbirds and small hawks that have been observed changing their migratory direction from southward to northward upon reaching this same spot during autumn migration (Wiedner *et al.* 1992). Ornithologists have speculated that most diurnally and at least some nocturnally migrating songbirds avoid crossing large bodies of open water such as the Delaware Bay at its mouth (*ca* 19 km) and instead cross such ecological barriers further inland at a narrower point (Wiedner *et al.* 1992; Berthold 1993). This is what green darners appeared to do. Individuals that had previously migrated southwesterly turned around in flight when over extensive open water and migrated northward. Doing so presumably allowed them to cross the Delaware Bay/Delaware River further upstream where the expanse of open water was considerably narrower (*ca* 4 km). Subsequently, the darners continued their migration southward into Delaware or Maryland.

Green darners—again like songbirds (Cochran *et al.* 2004; Cochran & Wikelski 2005)—did not appear to compensate strongly for wind direction but rather flew with the wind (±20°), in a pattern that is potentially different from tropical dragonflies crossing a lake (Srygley 2003). This behaviour makes sense if the migration rule about decreasing night-time temperatures ensures that individuals usually migrate when cold, northerly winds aid their southward migration. That is, decreasing night-time temperatures most probably indicate or predict favourable winds (Wikelski *et al.* 2003; Cochran & Wikelski 2005). Thus, a set of relatively simple decision rules may guide dragonfly migration, similar to the decision rules guiding songbird migration (Cochran & Wikelski 2005). These rules enabled migrating dragonflies to make significant southward advances during our study (12 km d$^{-1}$). This compares to a potential maximum daily advance of *ca* 200 km, assuming there was no wind and individuals flew for

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12 hours continuously at an observed ground speed of *ca* 5 m s$^{-1}$ (May 1995). Nevertheless, even at their observed modest average migration speed, green darners could advance over 700 km southward during an approximately two-month autumn migration season. Our data are consistent with calculations of migratory capabilities of green darners based on fat deposits. A 1 gram *Anax* carries roughly 300 mg of fat, or 12 000 J (May 1995). Estimated flight metabolism during foraging (probably more energy demanding than migratory flight because of speed and manoeuvres) is around 0.4 W g$^{-1}$ or 1440 J h$^{-1}$ for a 1 g insect (May 1995). Thus, a 1 gram darner may fly for a maximum of 8.3 h using stored fat. Migratory flight might become much more efficient if darners soar, which we consider likely, but have not confirmed yet by using continuous radio transmitters (Cochran & Wikelski 2005). Apparently, again like songbirds during overland migrations (Bowlin *et al.* 2005), green darners do not fly until all fat reserves are used, but rather fly for shorter times ensuring continuous fat availability even after migratory flights. The migration of green darners differs from that of birds in at least one fundamental respect, however; green darners observed migrating northward in the spring in North America do not exhibit much wing wear (Russell *et al.* 1998), strongly suggesting that they are not the same individuals involved in the autumn migration.

Our data demonstrate that it is now feasible to study medium- to long-range movement patterns in individual organisms as small as *ca* 1 g (Naef-Daenzer *et al.* 2005), a technique that has immediate biological (Taylor 1986; Hedin & Ranius 2002; Lorch *et al.* 2005; Sword *et al.* 2005), conservation (Simpkin *et al.* 2000), agricultural (Pedgley 1993) and economic implications (MacLeod *et al.* 2002). Signals from radio transmitters of the size used in our study could also be picked up from space (Swenson *et al.* 2004), and would thus make possible the global surveillance of small organisms (such as locusts) if a satellite system were installed (Swenson *et al.* 2004; Bowlin *et al.* 2005; Cochran & Wikelski 2005).

We are indebted to Bill Cochran, Christian Ziegler, NJ Audubon Society, Princeton airport (Nierenberg family) and the Hau–Wikelski laboratories. The study was supported by the National Geographic Society and the National Science Foundation (SGER). This paper is dedicated to our friends and colleagues Bill Cochran and George Swenson, pioneers of wildlife telemetry.

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