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ATYPICAL ECOLOGY OF *PANTALA FLAVESCENS* (FABR.) ON EASTER ISLAND (ANISOPTERA: LIBELLULIDAE)

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P. flavescens on Easter Island exhibits peculiar life history adaptations not documented from populations elsewhere. Adults seem to have abandoned the long-distance dispersal behaviour for which this circumtropical dragonfly species is notorious. They are relatively poor flyers, show a tendency to aggregate and forage in windsheltered areas, and display a perching reflex at sudden windrises. — The sp. reproduces in the major crater lakes, as well as in several smaller ponds that occur scattered around the island. In the crater lakes, young larvae are preyed upon by introduced *Gambusia* fish. Medium to fullgrown larvae escape predation (through protection provided by abdominal spines?), but are subject to chronic starvation because of the overall scarcity of suitable prey. — Selection for non-migrating behaviour may explain the behaviour of Easter Island *P. flavescens*. Poor larval nutrition is considered to have been the key epigenetic initiating factor.

INTRODUCTION

Eastern Island (27° 9'S, 109° 26'W), a Pacific Ocean intraplate volcanic island of small size (maximum length 22.5 km, maximum width 11.5 km, shape triangular) is noteworthy not only for its peculiar human culture, but also for its extreme isolation, hence truncated flora and fauna. Freshwater is not scarce on the island: three volcanic craters hold permanent lakes; numerous small ponds occur in depressions in the basaltic crust and collapsed lava tunnels; several rain-fed streamlets drain the flanks of the Terevaka volcano and consist of strings of stagnant water basins connected by a trickle of running water. However, the invertebrate fauna is extremely impoverished.

Aquatic microcrustaceans are reduced to one cladoceran, one cyclopoid copepod, and two or three ostracod species. Aquatic oligochaetes are represented by a small aelosomatid and possibly a tubificid. Coelenterata, Mollusca, Hirudinea, Hemiptera and Coleoptera are absent or so rare that they have, so far, escaped notice. Insects are represented by Diptera (mostly culicids) and the single dragonfly species *Pantala flavescens*.

As often, most of the species present in such a depauperate association may reach huge population densities. This applies to the cladocerans, ostracods, and must have been the case, to a nuisance level, with the culicids as well. In the 1930ies, the invertebrate eating cyprinodont fish *Gambusia* sp. was introduced to the major crater lakes of Rano Raraku and Rano Kau (Fig. 1). As a result, mosquito numbers on the island are now quite low, but the fish may have eliminated or reduced other faunal elements in these lakes as well. One of these is the notorious circumtropical migrant dragonfly *Pantala flavescens*, a conspicuous and well-known faunal element of the island (McE. KEVAN, 1965; CAMPOS & PENA, 1973; BELLE, 1990). Although quite common on the island, it presents several problems here which we comment upon hereunder.

We take pleasure in dedicating this paper to Dr B.F. Belyshev, at the occasion of his 80th birthday.

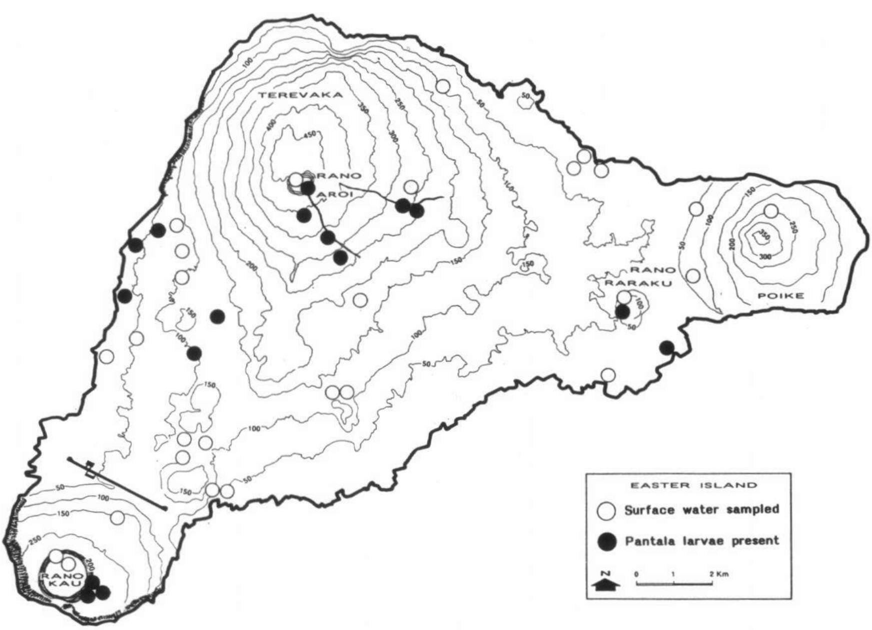

Fig. 1. Map of Easter Island showing all sampling stations (open circles. These include surface fresh waters, cave waters, and coastal brackish water), and waters where *Pantala* larvae were recorded (full circles).

OBSERVATIONS

The main body of observations was made between 15 Aug. and 3 Sep. 1990, but one of us (H.J.D.) also took some field notes during a previous visit (9-11 Feb. 1987) to the island. In addition, the information provided by BELLE (1990) for his visit (22-25 Nov. 1989) also turned out to be quite useful.

All these recent records span the period between August and February, i.e. from the coldest and wettest to the warmest and driest months (Tab. I). Since the climatic variations on the island are only slight, and *Pantala* was seen at every visit in numbers, we may assume that imagos are a permanent presence on the island, and that continuous reproduction occurs.

Table I
Easter Island climate: rainfall and temperature

	J	F	M	A	M	J	J	A	S	O	N	D	Year
Temp.	23.5	23.6	23.1	21.5	20.3	19.1	18.5	18.2	18.4	19.3	20.9	22.0	20.7
Rainf.	76.6	79.5	92.3	132.6	145.4	93.2	79.7	119.5	102.8	77.6	57.6	116.9	1197.3

In August 1990, there were numerous sightings of copulation and oviposition, while simultaneously we recorded the presence of young and full-grown larvae, emerging adults, and fresh and old exuviae.

We identified, and will offer comments, on two problems for *P. flavescens* on Easter Island, which are likely to be a challenge which this species does not meet elsewhere.

HUNGER

The extremely simple animal world indicated above severely limits the sources of food for *Pantala* larvae. While young instars may feed on the plankton crustaceans, there is little else for advanced instars to feed on than dipteran larvae. Figure 2 shows some of the habitats where larvae were actually collected. Although idyllic-looking, these sites were so poor in prey that they are comparable to deserts.

Circumstantial evidence for hunger was the observation of dead intermediate to large-sized larvae of *Pantala* in some of these sites. In the large crater lakes, where food was perhaps no problem, *Gambusia* certainly preys on *Pantala* larvae. Yet, in Rano Raraku several full-grown larvae were seen, which were apparently not harrassed by the numerous pupfish present.

This indicates that those few larvae which manage to outgrow a critical size, are no longer vulnerable to fish predation.

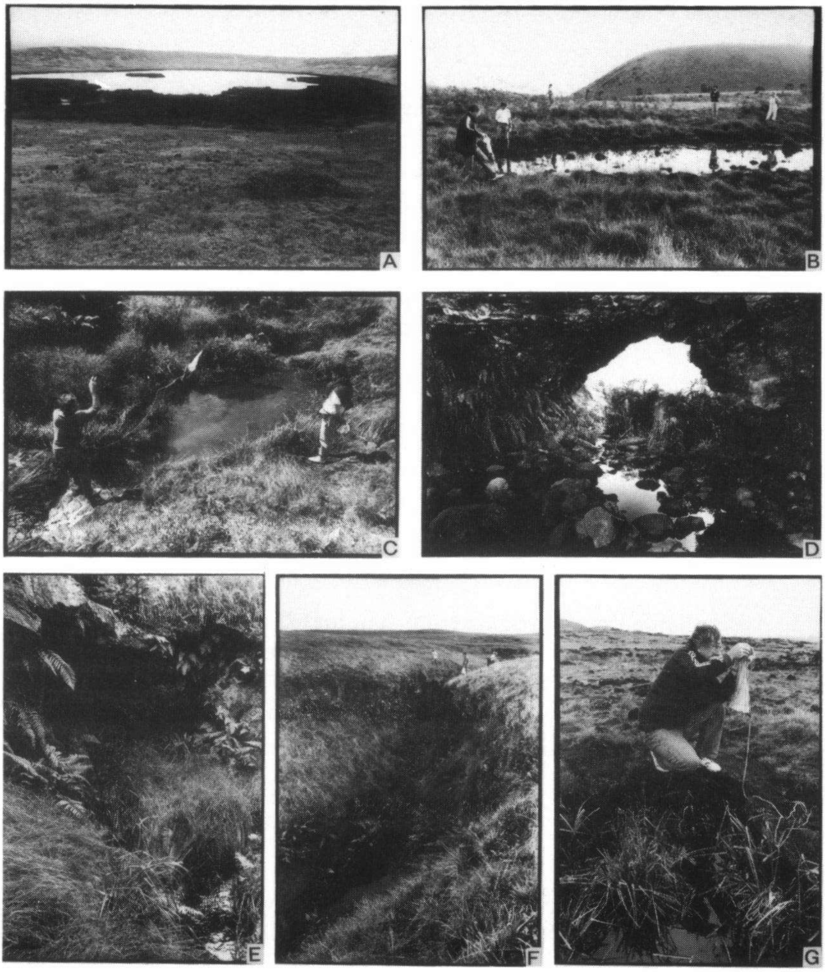

Fig. 2. Some aquatic ecosystems of Easter Island: (A) Rana Raraku crater lakes; — (B-C) Freshwater pools in basaltic cracks; — (D-F) Streamlet draining Mount Terevaka, and running partly underground (through lava tunnels: D, E), locally forming stagnant water basins (F); — (G) Small inundated lava cave. — Photograph by Patrick Dumont.

DISPERSAL

The behaviour of imagos on Easter Island differs from that seen elsewhere. Animals hardly ever fly vigorously, but tend to glide and hover at low altitudes at all times. Flight is so slow and hesitant that individuals may almost be captured by hand. Frequently, associations of large numbers of individuals (pseudoswarms) form on the leeward side of wood fringes and bushes. Wind on the island is as strong as unpredictable, often accompanied by rain, and *Pantala* disappears as soon as such storms occur. Shortly after rain, walking through long grasses and brushland, one may chase up scores of individuals that had sought refuge there.

DISCUSSION

Typically, *Pantala* imagos disperse away from their native pools immediately after emergence, and undertake long-distance migrations. Monsoon fronts and the associated winds are instrumental in carrying them across continental distances.

Nothwithstanding *Pantala's* notorious long-distance migration achievements, it is conceivable that the 3,800 km separating Easter Island from the South America mainland, combined with a lack of suitable stepping-stones in between, is well above the species' dispersal capabilities. Unaided immigration to the island is probably erratic and neglegible on a per generation basis. There is also no reason to believe that man introduced the dragonfly deliberately, but accidentally aided immigration (oceancrossing dragonflies landing on ships visiting the island) is likely to have become more important in historic times and may even lie at the very origin of *Pantala's* colonization of the island. Such occasional inputs of foreign genetic material are welcome as they favor the maintenance of genetic variation, but inputs apparently have never been so high as to hinder directional selection towards the unusual behaviour patterns.

Published information on the life history of *P. flavescens* in Africa and India indicates that long-distance migration shortly after emergence and during maturation is the rule (CORBET, 1962, 1988), and that residency does not constitute a typical feature of the species' life history adaptations (although it is likely to occur at an unspecified low level). Estimation of the possible strength of selection against the usual migrational behaviour thus becomes of particular importance in reasonings about population dynamics at the onset of colonization. The first filial (= first island-bred) *Pantala* population most probably represented the combined offspring of only a few — perhaps no more than one — reproducing pair(s) of successful immigrants. We may further assume that selection against dispersing behaviour is total, i.e. emigrants, successful or not, are lost to the island population, and when bearing in mind that immigration is infrequent and negligible on a per generation basis, it becomes clear that overall dispersing activity of the first generatons of island individuals would before long have led to extinction of Easter Island *Pantala*.

The apparent success of colonization actually implies that the strength of selection, as measured by the number of individuals eliminated each generation (in this case emigrating ones) was always surpassed by the population's reproductive output, as measured by the total number of surviving offspring of the selected (in this case resident) individuals. Consequently, a considerable portion of individuals in the first filial generations must already have exhibited the desired resident behaviour, instead of the usual dispersing behaviour.

All this strongly suggests that, despite their strong genotypic predisposition towards dispersal, the first island-bred *Pantala* must have experienced some epigenetic factor, during development, that increased the incidence of non-dispersing behaviour to a level above a vital threshold. Poor larval nutrition is the most likely candidate. Indeed, dragonfly larvae in Easter Island lakes and ponds might find just enough food to complete development, but may be uncapable of building up the fat reserves required for long-distance flight. Poor nutrition does not change the consequences of emigration for the island population (emigrating individuals, successful or not, are lost to the population), but might significantly increase the fraction of residents.

The hypothesis presented above allows the construction of a model in which migratory behaviour in *Pantala* is viewed as resulting from the combination of genotypic variance, in which recombination followed by selection drives the system towards more and more homozygosity for non-migrant behaviour, and environmental variance, in which nutritional conditions during development modify the behaviour of part of the individuals which would normally emigrate to a non-migratory status.

This system is reminescent of one encountered by DE MEESTER & DUMONT (1989) in studies on the phototactic behaviour of *Daphnia magna:* genotypes with fixed positive and negative phototaxis exist beside genotypes in which phototaxis is modifiable by hunger. Natural selection operating on natural populations changes the proportion of fixed to flexible genomes, and in certain conditions, the population may be driven close to a composition with only one genotype left.

Given enough time (but, as stated earlier, the age of the Easter Island *Pantala* is unknown, as is the incidence of occasional migrants that reach the island from South America and Polynesia and add genes to the population), its population gene pool should also evolve towards a genetically fixed non-migrant behaviour, with little variation left.

This hypothesis is testable, but will require considerable effort.

Comparisons can be made between the frequency of polymorphic loci for water-soluble proteins in continental and island populations. In spite of sexual recombination, the island population should display minimal variation. Better still, assuming a population in which migrant behaviour still arises at some frequency in each generation, a comparison between DNA restriction fragments of full-grown larvae and mature adults should produce an approximate measure of the rate of genome elimination per generation.

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REFERENCES

BELLE, J., 1990. A visit to the Easter Island. *Selysia* 19(1): 2.

CAMPOS, L. & L.E. PENA, 1973. Los insectos de Isla de Pasqua. *Revta chil. Ent.* 7: 217-229.

CORBET, P.S., 1962. *A biology of dragonflies.* Witherby, London.

CORBET, P.S., (Ed.), 1988. Current topics in dragonfly biology, 3. A discussion focusing on the seasonal ecology of Pantala flavescens in the Indian subcontinent. *Soc. int. odonat. rapid Comm.* (Suppl.) 8: viii+24 pp.

DE MEESTER, L. & H.J. DUMONT, 1989. Phototaxis in Daphnia: interaction of hunger and genotype. *Limnol. Oceanogr.* 34:1322-1325.

McE. KEVAN, D.K., 1965. The orthopteroid insects of Easter Island. *Ent. Rec. J. Var.* 77: 283-286.