A case study of an alien invertebrate (*Limnophyes pusillus*, Diptera, Chironomidae) introduced on Marion Island: Selective advantages

J.E. Crafford
Department of Entomology
University of Pretoria, Pretoria 0002

Limnophyes pusillus *Eaton was probably introduced into the sub-Antarctic from Europe at a very early date. It is firmly established on at least the Prince Edward and Kerguelen archipelagos.* L. pusillus *has been studied in detail on Kerguelen, and data on the life cycle and breeding biology of this species are summarised.* L. pusillus *is eminently preadapted to the sub-Antarctic terrestrial environment. Selective advantages include a long larval stage and parthenogenetic reproduction.*

Limnophyes pusillus *Eaton is waarskynlik in 'n baie vroeë stadium van Europa af na die sub-Antarktiese gebied ingevoer en is tans goed gevestig op sowel die Prins Edward- as die Kerguelen-eilandgroep.* L. pusillus *is op Kerguelen in besonderhede bestudeer en gegewens oor die lewensiklus en voortplantingsbiologie van die spesies is opgesom.* L. pusillus *is goed by sub-Antarktiese toestande aangepas. Van die selektiewe voordele wat hiertoe bydra, sluit 'n lang larfstadium en ongeslagtelike voortplanting in.*

Introduction

The order Diptera (flies and their kin) is well represented in the Antarctic and sub-Antarctic, constituting at least a quarter of the recorded insect fauna of this region. The family Chironomidae (midges) is particularly well represented. The only holometabolous insect occurring naturally on the Antarctic continent is the flightless chironomid midge *Belgica antarctica* (Peckham 1971); another flightless chironomid (*Halirytus amphibius* Eaton) is endemic to the islands of the Kerguelen Province.

Of the 33 insect species recorded from Marion Island, eight belong to the Diptera. Four of these, including *L. pusillus*, have a cosmopolitan distribution (Table 1), and were probably introduced onto the island by man (Jeannel 1953, Séguy 1971).

Many aspects of the biology of *L. pusillus* constitute preadaptations to the sub-Antarctic environment, and account for the marked success of the species on Marion Island. The biology and ecology of *L. pusillus* have been studied in detail on Kerguelen (Delettre & Trehen 1977, Delettre 1978, Delettre & Cancela da Fonseca 1979). Data on the life history and population dynamics of *L. pusillus* were mostly derived from this series of publications, but are supplemented by the results of an investigation on Marion Island (September 1984-April 1985). The latter investigation indicated that major aspects of the biology of *L. pusillus* (parthenogenesis, the year-long occurrence of mature larvae) are similar on the two islands.

History, biology and population dynamics of *Limnophyes pusillus* in the sub-Antarctic

L. pusillus was described by Eaton in 1875 from a specimen collected on Kerguelen (Dreux 1971). It was again collected on Kerguelen in 1903, and Enderlein (1908) considered the species to be endemic to the Kerguelen archipelago. *L. pusillus* is primarily a European species, however, and commonly occurs in oligotrophic Alpine lakes. It has also been recorded from the Canary Islands (Delettre and Trehen 1977). It was first collected on Marion Island by Jeannel in 1939. Both Jeannel (1953) and Séguy (1971) consider *L. pusillus* to have been introduced into the sub-Antarctic by man, probably at a very early date. Adult *L. pusillus* have in the past been collected in pollen traps on Marion Island (E.M.van Zinderen Bakker Sr *in litt.*). The species has also been recorded from nearby Prince Edward Island (this study), but not from the Crozet archipelago between Marion and Kerguelen. It is possible that the species has been overlooked on other sub-Antarctic islands; species lists from these islands are seldom complete.

Table 1
The Dipteran fauna of Marion Island

SPECIES	FAMILY	STATUS	DISTRIBUTION
Paractora dreuxi mirabilis Séguy	Helcomyzidae	Endemic	Marion and Prince Edward Islands
Apetenus litoralis Eaton	Coelopidae	Indigenous	Kerguelen Province Islands
Listriomastax litorea Enderlein	Coelopidae	Indigenous	Kerguelen Province Islands
Halirytus amphibius Eaton	Chironomidae	Indigenous	Kerguelen Province Islands
Limnophyes pusillus Eaton	Chironomidae	Alien	Cosmopolitan
Telmatoscopus albipunctatus Williston	Psychodidae	Alien	Cosmopolitan
Pericoma sp.	Psychodidae	Alien	Cosmopolitan
Fannia canicularis (L)	Muscidae	Alien	Cosmopolitan

Limnophyes pusillus reproduces parthenogenetically. Males are absent; the adult females are short-lived (7-14 days) and do not feed. Eclosion, egg-laying and hatching occur only during summer (December to May). The adults are poor flyers, taking to the air mostly on sunny days and at temperatures higher than 10 °C. Soon after eclosion a female lays a single egg-string of 80-100 eggs in any of a wide range of freshwater habitats. The eggs hatch within two days. There are four larval instars which last one, three, six and 41 weeks respectively. The major life stages of *L. pusillus* are illustrated in Figure 1.

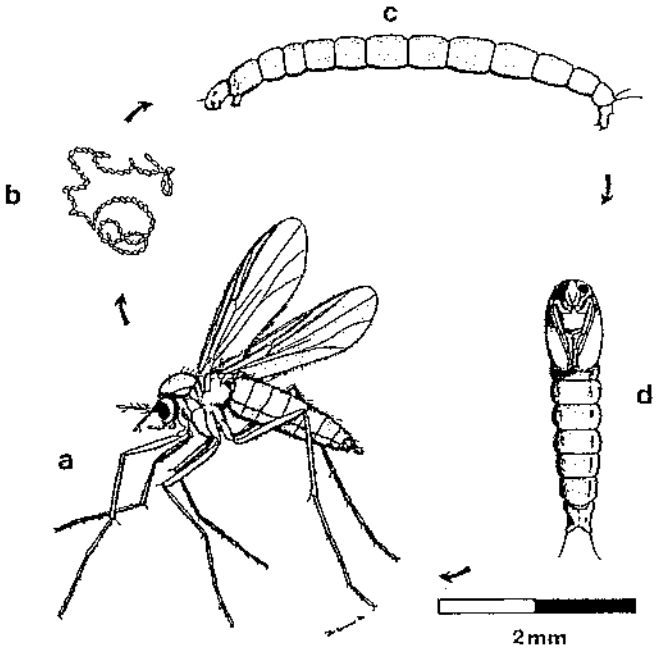

Fig. 1. Major life stages of *Limnophyes pusillus*. a. Adult female. b. Egg string. c. Mature larva. d. Pupa. (After data by Delettre & Trehen, 1977).

By June the fourth instar predominates in larval populations (Fig. 2). A stock of mature larvae is present at all times during the year. Larval growth, pupation, eclosion, and daily and seasonal emergence patterns are closely related to soil and air temperature, and often occur opportunistically in response to favourable temperatures.

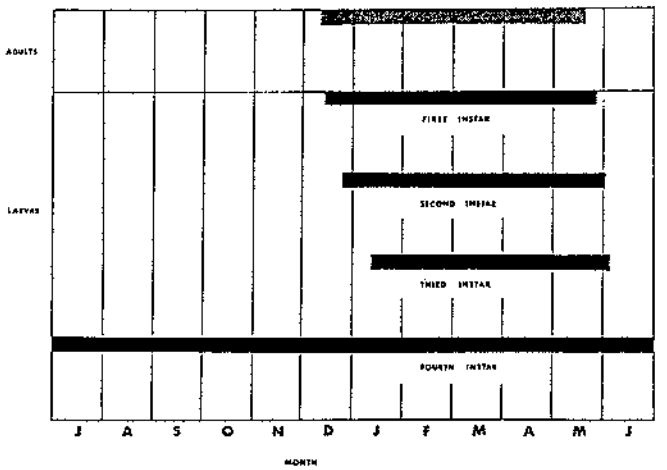

Fig. 2. The monthly occurrence of *Limnophyes pusillus* adults and larvae on Kerguelen (after data by Delettre & Trehen, 1977).

L. pusillus larvae are detritivorous. Adults vary much in size and coloration, probably as a result of differences in the nutrient status of detritus in different larval habitats. Populations associated with nutrient rich elephant seal wallows produce large, dark and robust adults. Adults from populations in oligotrophic lakes tend to be small, pale and delicate.

Discussion

The extraordinary success of *L. pusillus* on Marion Island should be seen against the background of the island environment (biotic and abiotic) and the adaptations of the indigenous insect fauna to this environment. (For an account of the environment, *vide* Van Zinderen Bakker *et al.* 1971).

The sub-Antarctic islands are characterised by impoverished, disharmonious and poorly integrated insect faunas (Carlquist 1974, Holdgate 1960). There is accordingly little interaction, virtually no competition and hardly any predation by invertebrate predators in these faunas (Downes 1964). Many habitats, including the entire freshwater biotope on Marion Island, are not colonised by indigenous faunal elements at all. *L. pusillus* is the only insect to have successfully colonised the freshwater habitat on Marion Island. It breeds in virtually all types of water bodies on the island, from lava lakelets to elephant seal wallows, and in most terrestrial habitats permanently saturated with water. In the rivers on Marion Island (there is only one perennial stream) *L. pusillus* larvae constitute the entire benthic fauna.

All the indigenous insects on Marion Island are characterised by long larval stages (Paulian 1953, Crafford 1984). The adults of most species are extremely short-lived, and are normally non-feeding, specialised reproductives. There is a marked tendency towards asexual reproduction. The indigenous flightless chironomid *Halirytus amphibius* reproduces parthenogenetically. In the case of the indigenous flightless Lepidoptera, eggs develop fully during the pupal stage and females emerge with most eggs already ripe. In all cases the less specialised, more adaptable larval stage predominates, and many species have generations spanning more than one year (Jeannel 1953).

Flightlessness and loss of swarming are probably the most striking adaptations to environmental conditions exhibited by the indigenous sub-Antarctic insect fauna. Darlington (1943) has shown that, on mountaintops, insects that lack flight are more viable than their winged counterparts, the former having simpler structure and metamorphosis and lower energy requirements. Downes (1964) demonstrated that, in the high Arctic, the major selective force for flightlessness (or loss of swarming) in insects is the need for 'economy of effort', since the insects generally show incomplete or poor metabolic adaptation to the low temperatures. Incomplete adaptation to low temperatures on the metabolic level is compensated for by economy of effort on all other levels. This economy is brought about by simplification of or withdrawal from activity on the ecological plane (Downes 1964). The result is a progressive lack of interaction on both the inter- and intraspecific levels (Table 2).

Conclusion

The success or failure of an 'alien' insect species introduced onto a sub-Antarctic island (or reaching the island by natural means of dispersal) would largely depend on how successfully

Table 2

Limnophyes pusillus on Marion Island: selective advantages presented by lack of activity on both inter- and intraspecific levels (see text).

INTERSPECIFIC	INTRASPECIFIC
1. Poor integration	1. Loss of swarming
2. Little interaction	2. Wing reduction
3. Little competition	3. Absence of males
4. No predation	4. Parthenogenesis

the species can compensate for poor adaptation to prevailing climatic conditions. *Limnophyes pusillus* is capable of effecting the economy of effort required as compensation for poor adaptation. On the interspecific level (Table 2) it is faced with a poorly integrated terrestrial fauna (selective advantages inherent in the island situation). On the intraspecific level it is pre-adapted to the sub-Antarctic environment (loss of swarm-

Acknowledgements

All biological research on Marion Island is carried out under the auspices of the South African Scientific Committee for Antarctic Research. The South African Department of Transport provides logistic and financial support.

References

CARLQUIST, S. 1974. Island Biology. Columbia University Press, New York.

CRAFFORD, J.E. 1984. Life cycle and kelp consumption of *Paractora dreuxi mirabilis* (Diptera:Helcomyzidae) : a primary decomposer of stranded kelp on Marion Island. *S. Afr. J. Antarct. Res.* 14: 18-22

DARLINGTON, P.J. 1943. Carabidae of mountains and islands: Data on the evolution of isolated faunas, and on atrophy of wings. *Ecol. Monogr.* 13: 37-16

DELETTRE, Y.R. 1978. Biologie et écologie de *Limnophyes pusillus* Eaton, 1875 (Diptera, Chironomidae) aux îles Kerguelen. I. Présentation générale et étude des populations larvaires. *Rev. Ecol. Biol. Sol.* 15(4): 475-486

DELETTRE, Y.R. & CANCELA DA FONSECA, J-P. 1979. Biologie et écologie de *Limnophyes pusillus* Eaton, 1875 (Diptera, Chironomidae) aux îles Kerguelen. II. Etude des populations imaginales et discussion. *Rev. Ecol. Biol. Sol* 16(3): 355-372

DELETTRE, Y.R. & TREHEN, P. 1977. Introduction à la dynamique des populations de *Limnophyes pusillus* (Diptera, Chironomidae) dans les sols des îles australes antarctiques françaises (Kerguelen). *Ecol. Bull. Swed. nat. Sci. Res. Coun.* No. 25: 80-89

DOWNES, J.A. 1964. Arctic insects and their environment. *Can. Entomol.* 96: 279-307

DREUX, Ph. 1971. Insecta. In: Marion and Prince Edward Islands; report on the South African biological and geological expedition 1965-1966. Eds E.M. van Zinderen Bakker Sr, J.M. Winterbottom and R.A. Dyer. A.A. Balkema, Cape Town. pp. 335-343.

ENDERLEIN, G. 1908. Die Insekten des Antarktischen Gebietes. *Deutsche Südpolar Expedition 1901-1903.* 10.

HOLDGATE, M.W. 1960. The fauna of the mid-Atlantic islands. *Proc. R. Soc. Lond. B Biol. Sci.* 152: 551-567

JEANNEL, R. 1953. Sur la faune entomologique de l'île Marion. *Rev. Fr. Entomol.* 20: 161-167

PAULIAN, R. 1953. Notes biologiques sur *Pringleophaga kerguelenensis* [sic] End. *Rev. Fr. Entomol.* 20: 45-47

PECKHAM, V. 1971. Notes on the chironomid midge *Belgica antarctica* Jacobs at Anvers Islands in the maritime Antarctic. *Pac. Insects Monogr.* 25: 145-166

SEGUY, E. 1971. Diptera. In: Marion and Prince Edward Islands; report on the South African biological and geological expedition 1965-1966. Eds E.M. van Zinderen Bakker Sr, J.M. Winterbottom and R.A. Dyer. A.A. Balkema, Cape Town. pp. 344-348.

VAN ZINDEREN BAKKER, E.M., WINTERBOTTOM, J.M. & DYER, R.A. (Eds.), 1971. Marion and Prince Edward Islands; report on the South African biological and geological expedition 1965-1966. A.A. Balkema, Cape Town.