Journal of Biogeography (1989) **16**, 345–351

Climate diagrams and biological control: an example from the areography of the ladybird *Chilocorus nigritus* (Fabricius, 1798) (Insecta, Coleoptera, Coccinellidae)

M. J. SAMWAYS *Department of Zoology and Entomology, University of Natal, Pietermaritzburg 3200, South Africa*

Abstract. *Chilocorus nigritus* (Fabricius, 1798) (Insecta, Coleoptera, Coccinellidae) is an important predator of many scale insects. The beetle is indigenous to the Indian sub-continent and Indo-China. In the late 1930s the beetle was introduced into Mauritius and the Seychelles. Since then it has spread rapidly to neighbouring islands and mainland Africa. Similarly, there has been an eastwards expansion into several of the Pacific Islands including the Solomons, Guam and New Caledonia. Recently, the beetle has also appeared in north-east Brazil, West Africa and Oman. Although the species is a good invader, it has specific climatic tolerances. Inland it is restricted to H. Walter's Zonobiome II, and in coastal areas to Zonobiomes I–II. The beetle was mass-reared and redistributed to specific localities in different Zonobiomes in Southern Africa. The species only established in Zonobiome II. With a knowledge of the biology of an invasive species and with Walter's climate diagrams, it is possible to predict where such a species will establish. Biocontrol programmes should consider climate diagrams prior to introduction of a new natural enemy, to determine the probability of success, at least with respect to climate.

Key words. *Chilocorus nigritus,* Coccinellidae, climate diagrams, areography, biological control.

INTRODUCTION

Classical biological control (CBC) involves searching for natural enemies of an exotic pest in the pest's native home. The material is then dispatched, quarantined and released against the pest, with the aim of reducing it to a new, low, economically insignificant level. Such a procedure has an element of chance, and success depends to a large extent on the skill and intuition of the biocontrol worker.

To improve the predictiveness of biocontrol projects, guidelines have been proposed based on logistic (Beirne, 1985), taxonomic, behavioural (Cock, 1986) and theoretical (Hassell, 1978) facets. Climate is often considered, but rarely quantified before natural enemies are introduced: although DeBach & Bartlett (1964), Greathead (1971) and Messenger & van den Bosch (1971) have pointed out the significance of climatic factors in determining the outcome of a biocontrol project. Franz (1964) goes further by pointing out that the ecological optimum for an effective natural enemy is only in the area of imperfect overlap of food plant distribution, suitable climate for the herbivore and suitable climate for the natural enemy. This means that a predatory species is not generally climatically adapted for controlling the pest over the whole of the infestation area (Hokkanen, 1985).

This paper examines these relationships in more detail using data gathered on the coccinellid *Chilocorus nigritus* (Fabricius, 1798) (Insecta, Coleoptera, Coccinellidae) (Fig. 1). R. G. Booth (pers. comm.) has pointed out that strictly the name should be *C. nigrita,* as Fabricius (1798) originally named it *Coccinella nigrita* and *'nigrita'* being a noun cannot change gender. However, as the beetle is so well-known by applied and ecological entomologists as *C. nigritus* this latter name is used here.

This species was chosen as it is conspicuous in the field, oligophagous on Homoptera, economically highly important and has been mass reared and disseminated to both climatically suitable and unsuitable areas (Samways, 1984, 1986; Samways & Tate, 1986). These factors together have resulted in a well-documented record of the beetle's historical distribution and expansion. Additionally, the pioneering climate-diagrams of Walter (1973, 1985), Walter & Leith (1960–67) and Walter *et al.* (1975) make possible direct comparisons of climate in different parts of the world. This background, plus new data, make it possible to build up an historical, present and futuristic areographic (*sensu* Rapoport, 1982) sketch of this important species.

METHODS

The historical distributional data were gathered from the literature and from the data labels of collected specimens. As the species is a conspicuous member of the insect fauna where it occurs, lack of specimens was a reasonable guide to

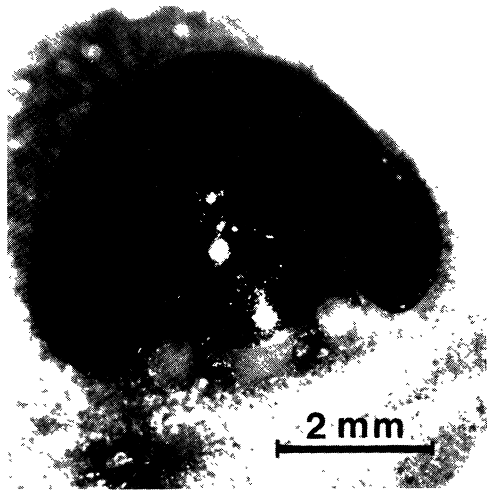

FIG. 1. Adult *Chilocorus nigritus* (F.). Note the distinctly hemispherical shapes and shiny black elytra. The frons and pronotal flaps are orange.

the species absence. This fact was given prominence when other usually rarer congenerics were obtained in the absence of *C. nigritus*.

From 10 September to 7 November 1986, Pakistan, India, Malaysia, Java, Australia, New Caledonia, Fiji, Mauritius and Réunion were visited to ascertain the abundance of the species. Abundance fell into three distinct, albeit arbitrary, categories: (1) The species was encountered on an almost hourly basis in the field, and often in congregating groups. (2) Occasional isolated individuals were encountered. (3) No individuals were seen.

Between 1982 and 1988 detailed records were kept of the species' distribution in Southern Africa (Mozambique, South Africa and Swaziland). Also in these years, the beetle was mass reared (up to 0.5 million eggs year^{-1} were produced) at the Outspan Citrus Centre, Nelspruit, Eastern Transvaal (Samways & Mapp, 1983; Samways & Tate, 1986). From this insectary material was regularly distributed around Southern Africa and dispatches were also made to Argentina and Israel.

Climatic data was obtained from Walter & Lieth (1960–67) and Walter *et al.* (1975).

OBSERVATIONS AND RESULTS

Geographical range prior to 1938

The centre of origin of *C. nigritus* appears to be the Indian sub-continent (Fig. 2). Its distribution is delimited by the Himalayan and Indo-China mountains in the north and east, and by the desert regions in the west. Prior to 1938, the beetle was regularly recorded from greater India (east coast, west coast, Tamil Nadu, Punjab, Maharashtra, Karmataka, Andra Pradesh, Orissa; Chatterjee & Bose, 1933; Crotch, 1874; Husain & Nath, 1927; Stebbing, 1903; Subramaniam, 1923; Woglum, 1913). Other countries where the species was recorded include Sri Lanka (Hutson, 1933), Burma, Sumatra (Korschefsky, 1910–32), China and Vietnam (Crotch, 1874). Crotch (1874) also mentions Japan, but Lewis (1896) points out that this is an error for *C. mikado* Lewis. Additionally, there are no other records for *C. nigritus* from Japan (H. Sasaji, pers. comm., 30 April 1987).

In about 1910, Woglum (1913) collected the species in India and introduced it to California and Florida, but it did not establish.

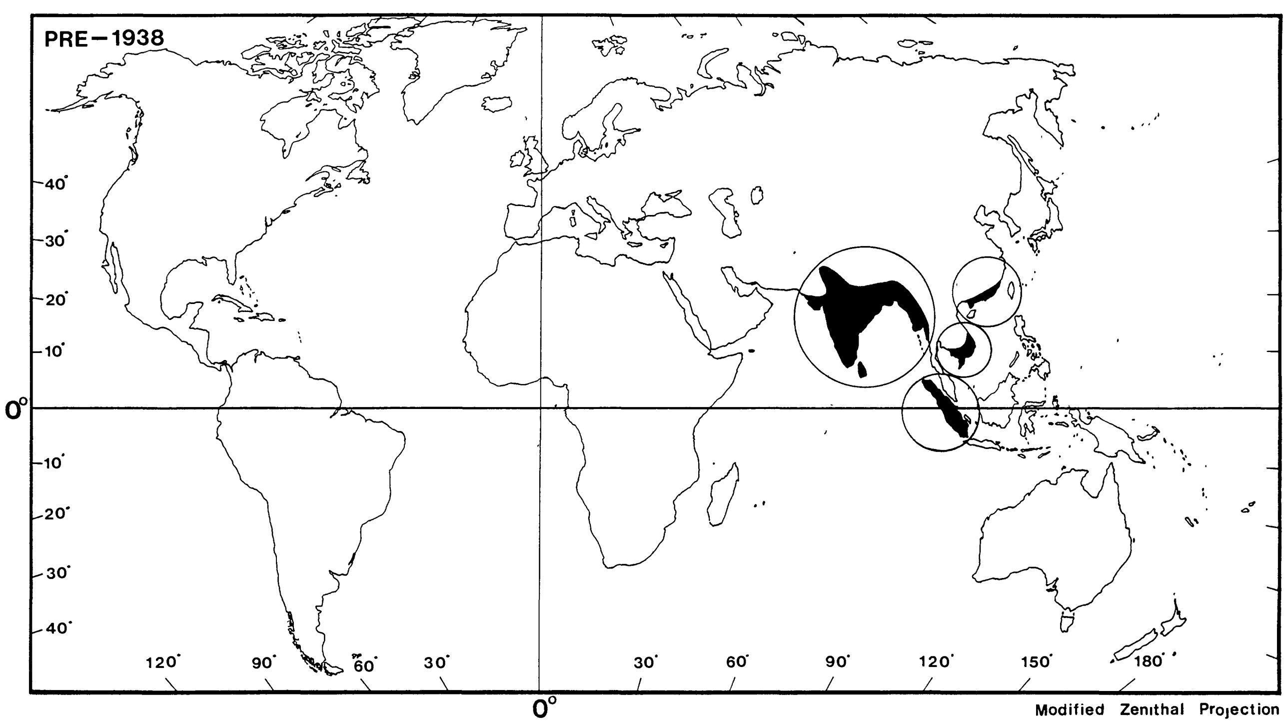

FIG. 2. Geographical range of *Chilocorus nigritus* (F.) from records and specimens pre-dating 1938.

Geographical range between 1939 and 1965

New records during this period include Sulawesi (Reyne, 1948), and modern-day Pakistan (but cf. Punjab above) except the high hills (Ahmad, 1970), coastal and sub-coastal areas, foothills and wet hills (Ghani & Muzaffar, 1974) and the country in general (Kazimi & Ghani, 1968). These are possibly new records rather than an expansion of range (Fig. 3).

The species was confirmed from India (east coast, west coast, Tamil Nadu (Tirumala Rao *et al.*, 1954), widespread, including south India and Punjab (Rahman, 1940), Uttar Pradesh (Sharga, 1948), Orissa (Kapur, 1940), Karnataka (Puttarudriah & Channa Basavanna, 1955), Tamil Nadu (Vesey-FitzGerald, 1953) and India in general (Puttarudriah & Channa Basavanna, 1953). Further confirmations also came from Sri Lanka (Davis, 1959) and China (Guangdong [Smith & Flanders, 1949]).

Trans-oceanic shipments of *Chilocorus nigritus*

In about 1910, Woglum (1913) collected the species in India and introduced it to California and Florida, but it did not establish. Of major significance was the shipment in 1938/39 of the beetle from Coimbatore in India to the Seychelles where it became firmly established (Vesey-FitzGerald, 1941, 1953), and also the successful introduction of the species into Mauritius from Sri Lanka in 1939 (Jepson, 1941; Moutia, 1944; Moutia & Mamet, 1946). In the mid-1950s, *C. nigritus* was also established on the Chagos Archipelago (Diego Garcia) from Mauritius (Orian, 1959). At the same time it was shipped from Mauritius to the Agalega Islands (Greathead, 1971). In the same area, it was introduced into Madagascar, probably from Mauritius, in the mid 1970s (J. R. Williams in Greathead & Pope, 1977).

In 1947, *C. nigritus* was introduced into Bermuda from Mauritius, but apparently did not establish (Bennett & Hughes, 1959). Similarly, in 1948, it was sent from Guandong Province in China to California but did not establish (Smith & Flanders, 1949). Twice the beetles were introduced into Hawaii (Oahu) firstly in 1958 from Sri Lanka (Davis, 1959) and then in 1971 from Guam (Davis, 1972). Today the beetle is firmly established (Leeper, 1976).

Geographical range expansion 1966–87

Since 1966, *C. nigritus* has dramatically increased its range both eastwards and westwards (Fig. 4). It has now been recorded from Java, Solomon Islands (Guadalcanal), Vanuatu (Espiritu Santo) (Chazeau, 1981), New Caledonia (Chazeau & Samways, pers. observ.), American Samoa (Gutierrez, 1978), Guam (Davis, 1972) and Society Islands (Tahiti, Huahine) (Delobel, 1978).

Westward expansion covers Réunion (Chazeau, Etienne & Fürsch, 1974), Aldabra (Hill & Blackmore, 1980), Madagascar (prior to 1972) (J. Chazeau, pers. comm.), Kenya, Tanzania (Greathead & Pope, 1977), South Africa (Georgala, 1979), Mozambique, Swaziland and Zimbabwe (Samways, 1984). The first mainland African records are those of specimens in the British Museum (Natural History) collection (Tanga, Tanzania, December 1966) and in the collection of H. Fürsch labelled Nairobi, Choromo, 19 April 1970. D. J. Greathead recorded it at Ramisi on the

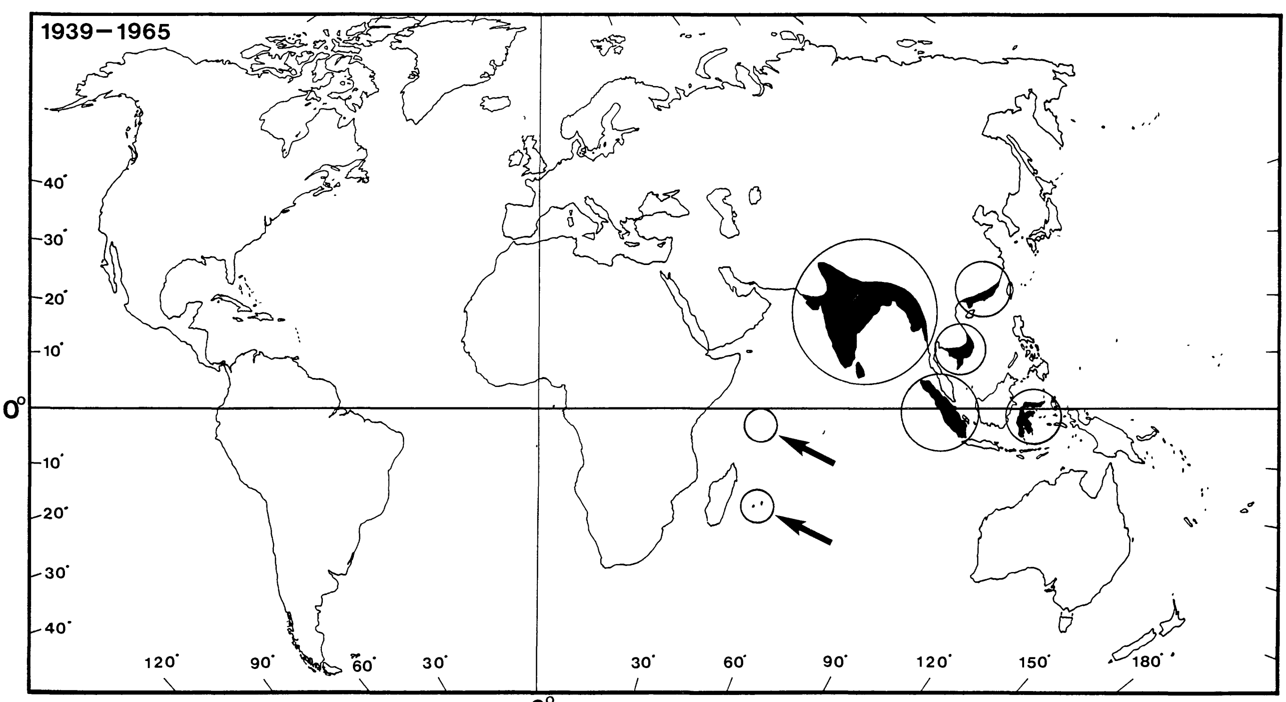

FIG. 3. Geographical range of *Chilocorus nigritus* (F.) from records and specimens collected between the years 1939 and 1965 inclusive. The eastwards expansion appears to be a 'natural' (but possibly phoretic on man's goods and transport) while the introduction into the Indian Ocean islands (arrowed) were planned biocontrol projects.

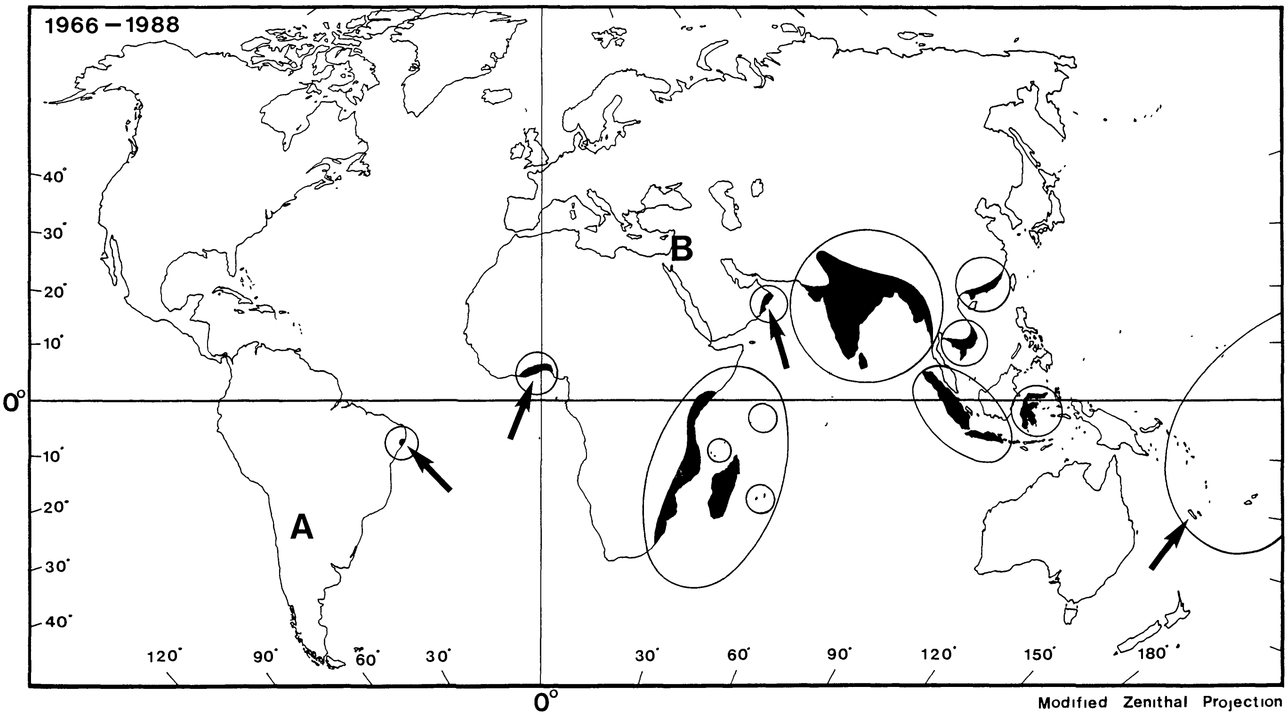

FIG. 4. Geographical range of *Chilocorus nigritus* (F.) from specimens and records collected between the years 1966 and 1988 inclusive. The species is present on many islands in the Pacific Ocean (right arrow) and on islands and continents surrounding the Indian Ocean. In 1983, the species was discovered in north-east Brazil (left arrow), and in 1984 in West Africa (centre left arrow) and further in 1987, in Oman (centre right arrow). In 1986 and 1987 respectively the beetle was dispatched from an insectary in the South African lowveld to insectaries in Argentina (A) and Israel (B).

Kenya coast in 1968, at Arusha Chini (Tanzania) in 1969, and at Gonza (Tanzania) in 1970 (Greathead & Pope, 1977).

Of particular interest is the recent confirmation (by specimens collected by J. P. Morin in February 1983 and identified by J. Chazeau) that the species has established in Pernambuco, north-east Brazil. Also, the beetle has recently appeared (December 1984) at Anacho in Togo (West Africa) and (September 1986) at the University of Cape Coast in Ghana, and in Oman (1987) (specimens determined by R. G. Booth).

Rearing and dissemination of *Chilocorus nigritus* in southern Africa

The beetle was first reared at Letaba Estates near Tzaneen in the northern Transvaal. In 1982, a mass-rearing facility was created in Nelspruit in the eastern Transvaal and from there material was dispatched to many parts of southern Africa, principally for control of *Aonidiella aurantii* (Maskell). This resulted in an annual increase in its range, and by 1986 the beetle was firmly established in all the sub-tropical areas as far south as the Nkwalini Valley in Natal (Fig. 5). Despite introduction of many hundreds of thousands of eggs, larvae and adults into the central Transvaal, eastern and western Cape, the beetle did not establish.

On 22 May 1986, 150 adults and about 5000 eggs were dispatched to San Miguel de Tucuman, Argentina, where they are now being reared. On 2 March 1987, fifty larvae and 100 adults were sent to Rehovot, Israel, where they are presently being reared.

Chilocorus nigritus abundance in the eastern hemisphere in 1986

C. nigritus was present in large numbers at Rawalpindi (Pakistan), Poona and Bangalore (India), and in small numbers in the foothills of the Himalayas (<1500 m) 50 km north of Murree (Pakistan), Madras (India), Noumea (New Caledonia) and Reunion (<500 m). Despite intensive searches, it was not found in the North-West Frontier Province (Pakistan), Malaysia, Java or Fiji. Specimens from Pakistan in 1986 freely interbred with Eastern Transvaal specimens in the laboratory in 1987.

Chilocorus nigritus, abundance and climatic types

The sites in the Indian sub-continent where *C. nigritus* is abundant fall within Walter's (1973) Zonobiome II (Table 1). This is a tropical and frost-free zone with a distinct annual temperature cycle. Heavy zenithal rains occur in the warm perhumid summer season and there is an extremely dry and cool winter season. In some extreme years, the occasional light frost occurs in low-lying valleys. This zone extends from about 10°N to 30°N and 5°S to 30°S. The Pacific Islands on which the species occurs are those with a wet season (e.g. Guam, Noumea in New Caledonia) and an

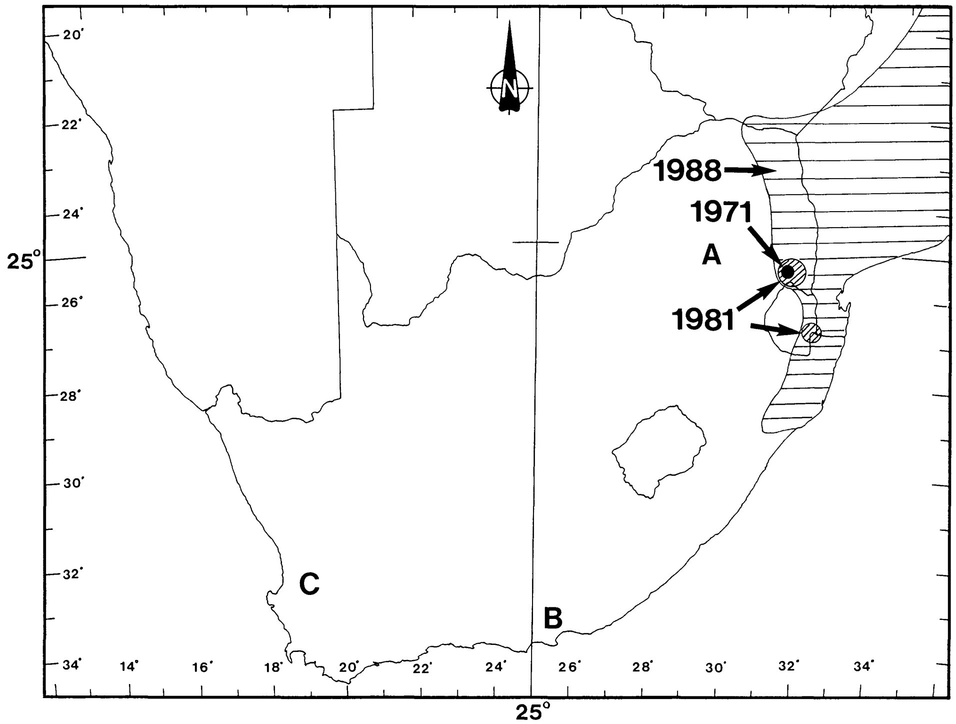

FIG. 5. Increasing geographical range of *Chilocorus nigritus* (F.) during the 1970s and 1980s in southern Africa. The beetle was reared in the South African lowveld (close to the site where it was first discovered in 1971) and dispatched to various localities. Despite intensive introductions, the species did not establish in area A (central-northern Transvaal), B (eastern cape) and C (western Cape).

island dry season which is not as dry as on the mainland. Additionally, *C. nigritus* has been found occasionally in Zonobiome I. The species does not extend into Zonobiome III. In summer, it can occur up to altitudes of 2000 m in Zonobiomes I and II. The striking feature is the match between the beetle's distribution and climatic types.

The climatic regions invaded by the species in Africa are again Zonobiome II, although the beetle has not yet been found above 800 m and does not occur in the frost-prone highveld in central southern Africa (compare Walter's (1973) Fig. 5 with Fig. 4 here).

The South American site (Pernambuco) where *C. nigritus* has been found also falls within Zonobiome II.

Climatic zones where *Chilocorus nigritus* has not established

Fig. 4 shows three areas in Southern Africa (central Transvaal, eastern Cape and western Cape) where *C. nigritus* has been introduced in large numbers but has not established (Samways, 1984). The central Transvaal has regular light frosts and is mostly at about 1000 m elevation. Although this area falls within Zonobiome II, the altitude makes this part of the Zonobiome unsuitable for permanent establishment of the species. Similarly, the western Cape (Zonobiome IV) and the eastern Cape (Zonobiome V) are also unsuitable. Zonobiome IV (Capensic) is characterized by cool, wet winters and hot, dry summers. Zonobiome V is a transitional zone between the tropical-subtropical and typical temperate zones, although inland the climate in some localities tends to a type III.

TABLE 1. Continental and island sites where *Chilocorus nigritus* (F.) is abundant, either indigenously or after introduction by Man.

Continental (Zonobiome II)		Island (Zonobiome I–II)	
Indian region (Indigenous)	Africa (Invaded)	Indian Ocean (Introduced and invaded)	Pacific Ocean (Introduced and invaded)
Rawalpindi	Malelane	Mauritius	Noumea
Poona	Komatipoort	Seychelles	Guam
Bangalore	Big Bend	Réunion	Vanuatu
Cuttack	Pongola	Aldabra	Oahu

DISCUSSION

Origins of the species

Being highly apparent in the field, especially when congregating, early records of *C. nigritus* are probably reliable. The only doubtful record is that of Japan (Crotch, 1874). Possibly also, there is a morphologically similar but rarer species occurring within the overall range of *C. nigritus* in Sri Lanka and the Lakshadweep Islands (R. G. Booth, pers. comm.). The centre of abundance is the Indian subcontinent, particularly where the banyan tree (*Ficus benghalensis* L.) is present. This tree has a major attraction for the beetle, which uses it for congregating (Ketkar, 1959). Being principally Indian, the range originally extended from 35°N to 5°S, and limited in the west by arid Baluchistan and southern Afghanistan, in the north by the Himalayas, and in the south and east by the oceans.

Chilocorus nigritus in the western Indian Ocean region

Deliberate transportation of the beetle from the Indian region to the Seychelles and particularly Mauritius, extended the species distributional range to 20°S and placed it on the western side of the Indian Ocean. The biological significance of these introductions is that they illustrate the good colonizing ability of the beetle, even with a change from the northern to the southern hemisphere.

Within 40 years the beetle then spread to the neighbouring islands of Réunion, Aldabra and Madagascar. An extension of the westward expansion was the appearance on mainland Africa simultaneously in central and southern Africa in the mid/late 1960s. This further emphasized the beetle's remarkable colonizing ability.

An important factor in its establishment in southern Africa is that in the mid-1970s one of its hosts (*A. aurantii*) had become resistant to organophosphate insecticides (Nel, De Lange & Van Ark, 1979), and was present in great abundance at the time. This fact is supported by the beetle later becoming a dominant feature of the natural enemy fauna in citrus and causing a highly significant economic impact (Samways, 1984, 1988).

Means of dispersal

Eggs are laid in various places on the host plant, but a particularly attractive site is among the fibres of spiders' webs (Samways & Mapp, 1983). Hatching larvae feed on the nearby host scale insects. Larvae on fruit which is picked and transported, are readily redistributed, as are adults after settling on vertical structures on ships. In this way the beetle can easily spread along shipping lanes. In New Caledonia, *C. nigritus* was first observed at Noumea yachting harbour. Similarly, the first African and South American records are directly inland from major ports (Mombasa, Maputo and Recife). The spread to various islands in the Indian Ocean may possibly have been on yachts island-hopping.

Within southern Africa, the range has increased through natural dispersal and deliberate spread. In the appropriate climatic areas where host scale is abundant, the beetle has readily established. But after introduction into climatically unsuitable areas it soon died out. The appropriate climate is Zonobiome II (Walter & Lieth, 1960–67) up to 800 m. Outside this Zonobiome, and above this altitude, the climate is unsuitable.

Future spread

C. nigritus has been redistributed to insectaries at Rehovot in Israel and San Miguel de Tucuman in Argentina. As the species is limited in its latitudinal spread, it is likely that these two localities (32°N for Israel and 27°S for Argentina) may be marginal. Of the two sites, San Miguel is favoured climatically as it falls within Zonobiome II. Rehovot is probably unsuitable (as was California) as this is Zonobiome IV. Similarly, as the beetle has established within Zonobiome II in Pernambuco, Brazil, and as a larger part of central and eastern South America falls within this Zonobiome, the species is quite likely to spread across this belt in frost-free areas from San Miguel in the south-west to Pernambuco in the north-east. Similarly, as it has very recently appeared in coastal Togo and Ghana, it is likely to spread to other areas of West Africa (Senegal, The Gambia, Guinea-Bissau) with a Zonobiome I–II climate.

As *C. nigritus* has appeared on several Indonesian and South Pacific islands with a Zonobiome I–II climate, the species is quite likely to invade other areas with a similar climate. Such areas include northern Australia, Central America (parts of Mexico e.g. Jalisco, Tamaulipas, Yucatan) and the Caribbean (e.g. southern Cuba and Haiti). If diaspid scale insects become an economic problem in this area, *C. nigritus* appears to be a promising agent.

Climate diagrams have shown where *C. nigritus* is likely to establish, extrapolating from areas where it has already invaded. Climate diagrams are appropriate in this case because the insect is climatically sensitive and oligophagous, which means that its range is restricted by physical conditions rather than by food. For more diet-restricted natural enemies, the climatic tolerances of the host also must be taken into account.

ACKNOWLEDGMENTS

I thank Professor Drs Hemut Fürsch and Hiroyuki Sasaji and Dr R. G. Booth for providing information from specimens in their collections. Thanks also to Mrs Ann Best for typing the manuscript. The South African Co-operative Citrus Exchange, the University of Natal Research Fund and the Foundation for Research Development (C.S.I.R.) generously funded fieldwork and museum visits.

REFERENCES

Ahmad, R. (1970) Studies in West Pakistan on the biology of one nitidulid species and two coccinellid species (Coleoptera) that attack scale insects (Hom., Coccoidea). *Bull. ent. Res.* **60,** 5–16.

Beirne, B.P. (1985) Avoidable obstacles to colonization in classical biological control of insects. *Can. J. Zool.* **63,** 743–747.

Bennett, F.D. & Hughes, I.W. (1959) Biological control of insects pests in Bermuda. *Bull. ent. Res.* **50,** 423–436.

Chatterjee, N.C. & Bose, M. (1933) Entomological investigations on the spike disease of sandal (17). Coccinellidae (Col.) Supplementary data. *Ind. For. Rec.* **19,** 1–10.

Chazeau, J. (1981) La lutte biologique contre la cochenille transparente du cocotier *Temnaspidotus destructor* (Signoret) aux Nouvelles-Hebrides (Homptère, Diaspididae). *Cahiers O.R.S.T.O.M., Serie Biologique,* **44,** 11–22.

Chazeau, J., Etienne, J. & Fürsch, H. (1974) Les Coccinellidae de l'île de la Réunion (Insecta, Coleoptera). *Bull. Mus. Nat. d'Hist. Natur.,* 3e Serie, No. 210, 1–297.

Cock, M.J.W. (1986) Requirements for biological control: an ecological perspective. *Biocontrol News Inform.* **7,** 7–16.

Crotch, G.R. (1874) *A revision of the coleopterous family Coccinellidae.* Janson, London.

Davis, C.J. (1959) Recent introductions for biological control in Hawaii – IV. *Proc. Hawaiian Ent. Soc.* **17,** 62–69.

Davis, C.J. (1972) Recent introductions for biological control in Hawaii – XVII. *Proc. Hawaiian Ent. Soc.* **21,** 187–190.

DeBach, P. & Bartlett, B.R. (1964) Methods of colonization, recovery, and evaluation. *Biological control of pests and weeds* (ed. by P. DeBach), pp. 402–426. Reinhold, New York.

Delobel, A. (1978) Contribution à la connaisance de l'entomofaune d'incidence économique en Polynesie Française. Office de la Recherche Scientifique et Technique Outre-Mer, Centre de Noumea, Nouvelle Caledonie., mimeographed report 47 pp.

Fabricius, J.C. (1798) *Supplementum entomologiae systematicae.* Apud Proft & Storch, Hafnia.

Franz, J.M. (1964) Dispersion and natural-enemy action. *Ann. appl. Biol.* **53,** 510–515.

Georgala, M.B. (1979) Investigations on the control of the red scale *Aonidiella aurantii* (Mask.) and citrus thrips *Scirtothrips aurantii* Faure on citrus in South Africa. *Annale, Univ. van Stellenbosch, Serie A3 (Landbou),* **1,** 1–179.

Ghani, M.A. & Muzaffar, N. (1974) Relations between the parasite–predator complex and the host-plants of scale insects in Pakistan. Commonwealth Institute Biological Control Miscellaneous Publication No. 5, 92 pp.

Greathead, D.J. (1971) A review of biological control in the Ethiopian Region. Commonwealth Institute of Biological Control Technical Communication No. 5, 162 pp.

Greathead, D.J. & Pope, R.D. (1977) Studies on the biology of some *Chilocorus* spp. (Coleoptera: Coccinellidae) preying on *Aulacaspis* spp. (Hemiptera: Diaspididae) in East Africa, with the description of a new species. *Bull. ent. Res.* **67,** 259–270.

Gutierrez, J. (1978) Biological control of the coconut hispid (*Brontispa longissima*) and a survey of fruit flies in American Somoa. South Pacific Commission, Noumea, New Caledonia, mimeographed report December 1978, 10 pp.

Hassell, M.P. (1978) *The dynamics of arthropod predator–prey systems.* Princeton University Press.

Hill, M.G. & Blackmore, P.J.M. (1980) Interactions between ants and the coccid *Icerya seychellarum* on Aldabra atoll. *Oecologia,* **45,** 360–365.

Hokkanen, H. (1985) Success in classical biological control. *CRC Crit. Rev. Plant Sci.* **3,** 35–72.

Husain, M.A. & Nath, D. (1927) The citrus psylla (*Diaphorina citri,* Kuw.) (Psyllidae: Homoptera). *Mem. Dept. Agric., Ind. Ent.,* 5–27.

Hutson, J.C. (1933) The coconut scale (*Aspidiotus destructor). Trop. Agric. Ceylon,* **80,** 254–256.

Jepson, W.F. (1941) 1. Pests of sugarcane. *Ann. Rep. Ent. Div., Rep. Dept. Agric., Mauritius,* **1939,** 16–19.

Kapur, A.P. (1940) A note on the ladybird beetles (Coccinellidae) predating upon the cane white-fly, *Aleurolobus barodensis* Mask. *Curr. Sci.* **9,** 134.

Kazimi, S.K. & Ghani, M.A. (1968) A list of Coccoidea of Pakistan and their natural enemies. *Commonwealth Inst. Biol. Contr. Tech. Bull.* **3,** 31–39.

Ketkar, S.M. (1959) Mass assemblage of the coccinellid beetle *Chilocorus nigritus* Fabr. on banyan trees in Poona. *Sci. Cult.* **25,** 273.

Korschefsky, R. (1932) *Coleopterorum Catalogus,* 16 (S. Schenking (Ed.). Berlin), Pars 120, p. 240. W. Junk.

Leeper, J.R. (1976) A review of the Hawaiian Coccinellidae. *Proc. Hawaiian Ent. Soc.* **22,** 279–306.

Lewis, G. (1896) On the Coccinellidae of Japan. *Ann. Mag. nat. Hist.* (Ser. VI), **17,** 22–41.

Messenger, P.S. & van den Bosch, R. (1971) The adaptability of introduced biological control agents. *Biological control* (ed. by C. B. Huffaker), pp. 68–92. Plenum, New York.

Moutia, L.A. (1944) The sugar-cane scale, *Aulacaspis tegalensis,* Zeht. *Bull. ent. Res.* **35,** 69–77.

Moutia, L.A. & Mamet, R. (1946) A review of twenty-five years of economic entomology in the island of Mauritius. *Bull. ent. Res.* **36,** 439–472.

Nel, J.J.C., De Lange, L. & Van Ark, H. (1979) Resistance of citrus red scale, *Aonidiella aurantii* (Mask.) to insecticides. *J. ent. Soc. sth. Afr.* **42,** 275–281.

Orian, A.J.E. (1959) Report on a visit to Diego Garcia. *Rev. Agric. Sucr.* **38,** 127–143.

Puttarudriah, M. & Channa Basavanna, G.P. (1953) Beneficial coccinellids of Mysore – I. *Ind. J. Ent.* **15,** 87–96.

Puttarudriah, M. & Channa Basavanna, G.P. (1955) Beneficial coccinellids of Mysore – II. *Ind. J. Ent.* **17,** 1–5.

Rahman, K.A. (1940) Important insect predators of India. *Proc. Ind. Acad. Sci.* **12(B),** 67–74.

Rapoport, E.H. (1982) *Areography, geographical strategies of species.* Pergamon Press, Oxford.

Reyne, A. (1948) Studies on a serious outbreak of *Aspidiotus destructor rigidus* in the coconut-palms of Sangi (North Celebes). *Tijd. Ent.* **89,** 83–123.

Samways, M.J. (1984) Biology and economic value of the scale predator *Chilocorus nigritus* (F.) (Coccinellidae). *Biocontr. News Inform.* **5,** 91–105.

Samways, M.J. (1986) Combined effect of natural enemies (Hymenoptera: Aphelinidae & Coleoptera: Coccinellidae) with different niche breadths in reducing high populations of red scale, *Aonidiella aurantii* (Maskell) (Hemiptera: Diaspididae). *Bull. ent. Res.* **76,** 671–683.

Samways, M.J. (1988) A pictorial model of the impact of natural enemies on the population growth rate of the scale insect *Aonidiella aurantii. S. Afr. J. Sci.* **84,** 270–272.

Samways, M.J. & Mapp, J. (1983) A new method for the mass-introduction of *Chilocorus nigritus* (F.) (Coccinellidae) into citrus orchards. *Citrus Subtrop. Fr. J.* **598,** 4–6.

Samways, M.J. & Tate, B.A. (1986) Mass-rearing of the scale predator *Chilocorus nigritus* (F.) (Coccinellidae). *Citrus Subtrop. Fr. J.* **630,** 9–14.

Sharga, V.S. (1948) Biological control of some hemipterous insect pests of crops in India. *Curr. Sci.* **17,** 302–303.

Smith, H.S. & Flanders, S.E. (1949) Recent introductions of entomophagous insects into California. *J. econ. Ent.* **42,** 995–996.

Stebbing, E.P. (1903) Notes upon the known predaceous Coccinellidae of the Indian Region, Part 1. *Ind. Mus. Notes,* **6,** (1), 55.

Subramaniam, T.V. (1923) Some coccinellids of South India. *Proc. Fifth Ent. Meet., Pusa,* Part 18, 108–118.

Tirumala Rao, V., Leela David, A. & Mohan Rao, K.R. (1954) Attempts at the utilisation of *Chilocorus nigritus* Fab. (Coleoptera, Coccinellidae) in the Madras State. *Ind. J. Ent.* **16,** 205–209.

Vesey-FitzGerald, D. (1941) Progress of the control of coconut-feeding Coccidae in Seychelles. *Bull. ent. Res.* **32,** 161–164.

Vesey-FitzGerald, D. (1953) Review of the biological control of coccids on coconut palms in the Seychelles. *Bull. ent. Res.* **44,** 405–413.

Walter, H. (1973) *Vegetation of the earth, and ecological systems of the geo-biosphere.* Springer, New York.

Walter, H. (1985) *Vegetation of the earth, and ecological systems of the geo-biosphere,* 3rd edn. Springer, New York.

Walter, H., Harnickell, E. & Mueller-Dombois, D. (1975) *Climate-diagram maps of the individual continents and the ecological climatic regions of the earth.* Springer, Berlin.

Walter, H. & Lieth, H. (1960–67) *Klimadiagramm-welt atlas.* Gustav-Fischer, Stuttgart. 8000 stations.

Woglum, R.S. (1913) Report on a trip to India and the Orient in search of the natural enemies of the citrus white fly. *U.S.D.A., Bur. Ent., Bull.* No. 120, 58 pp.