ASPECTS OF THE COMPARATIVE ECOLOGY OF POPULATIONS OF FOUR *PATROBUS* SPECIES (COLEOPTERA: CARABIDAE: PATROBINI) AT GEORGE LAKE, ALBERTA

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ABSTRACT

Way of life and use of habitats by Patrobus stygicus *Chaudoir,* P. lecontei *Chaudoir,* P. foveocollis *Eschscholtz, and* P. septentrionis *Dejean were studied and compared with previously hypothesized phylogenetic relationships of these species. Larvae and adults of* P. foveocollis *were least hygrophilous and ranged from forest margins through sedge meadows to* Salix *habitats adjoining the marshes. Larvae and adults of* P. stygicus *were most hygrophilous and ranged from forest margins through shallow marsh to the lakeside. Adults and larvae of* P. lecontei *ranged from forest margins to shallow marsh. Most adults of* P. septentrionis *were found in sedge meadows; their larvae were not recovered. Adults of* P. lecontei *were characterized by rapid development of sexual maturity and a short life, whereas adults of* P. stygicus *had a longer prereproductive period and a longer life. Possible evolutionary significance of the ecological characters specified above and their consequences are discussed for the North American species of* Patrobus.

RÉSUMÉ

La vie et l'usage de l'habitat de Patrobus stygicus *Chaudoir,* P. lecontei *Chaudoir,* P. fovoecollis *Eschscholtz, et* P. septentrionis *Dejean ont été étudiés et comparés quant aux relations phylogénétiques. Les larves et les adultes de* P. foveocollis *étaient le moins hygrophiles et s'étendaient depuis des clairières, à des Lisières, des pâtis couverts de laîches, jusqu' aux habitats* Salix *contigus aux marécages. Les larves et les adultes de* P. stygicus *étaient le plus hygrophiles et s'étendaient depuis des lisières, à des marécages peu profonds jusqu'aux bords d'un lac. Les* Patrobus lecontei *larves et les adultes s'étendaient des lisières aux marécages peu profonds. Les adultes de* P. septentrionis *se trouvaient dans la plupart des cas dans des pâtis couverts de laîches; leurs larves n'ont pas été trouvées. Les adultes de* P. lecontei *étaient caractérisés par un développement rapide de maturité sexuelle et d'une vie courte, tandis que les adultes de* P. stygicus *avaient une période adulte prérêproductive plus longue et une vie plus longue. La signification évolutionnaire possible des caractéristiques écologiques mentionnées ci-dessus et leurs conséquences ont été traitées, en se limitant aux espèces* Patrobus *nord-américaines.*

INTRODUCTION

Little is known of the natural history of the majority of North American carabid beetles. However, the excellent taxonomic revision of Canadian, and Alaskan carabids by Lindroth (1961-1969) and studies by Darlington (1938) and by Ball and associates (for example, Ball, 1966) have paved the way for field and laboratory investigations. Few North American workers have studied the comparative ecology of closely related carabid species, for example from the same subgenus, in an attempt to define ecological and behavioural characters which are useful

in taxonomy and phylogeny.

Populations of four *Patrobus* species (*P. stygicus*, *P. lecontei*, *P. foveocollis* and *P. septentrionis*) which frequent wet boreal habitats are considered in this study. The objectives of this study were to use ecological characters to test taxonomic and phylogenetic hypotheses about closely related species and to compare their habitat use.

The following questions were asked:

(1) Are these *Patrobus* species separated in space during their period of main activity?

(2) Are populations of different species, that occur in the same general habitats, separated by seasonal activity?

(3) Does spatial distribution of these carabids vary according to time of year?

Life history features were considered as adaptations (Cole, 1954). Evolutionary interpretation of these features and other ecological characters were tested against Darlington's (1938) hypotheses about relationships of these species, with the exception that *P. fossifrons* and *P. stygicus* are regarded as distinct species rather than subspecies (see Lindroth, 1961).

THE FIELD STATION AND STUDY AREAS

The Field Station

The study area is at 53° 57′N and 114° 06′W at George Lake, about 64 km northwest of Edmonton, Alberta. The area is at the southern margin of the boreal mixed forest subzone (La Roi, 1968). Graham (1969) described the main vegetation zones.

Main Habitat Types and Study Areas

Habitats were classified by indicator plant species (Elton and Miller, 1954) and changes in water level within and between years were noted. Wet habitats (Figure 1) were classified as marsh or transition zone.

MARSH ZONE. – There were two main marsh habitats: (a) deep marsh was characterized by a floating mat of *Typha latifolia* L. which extended from lakeside to shallow marsh; this subzone corresponds with reed swamp as defined by Moss (1953,1955); (b) shallow marsh which extended from deep marsh to *Salix* habitats in the transition zone. It consisted of tussocks of *Carex* species among pools; leading dominants included *Carex aquatilis* Wahlenb. and *C. rostrata* Stokes

TRANSITION ZONE. – Transition zones were delimited readily by shallow marsh on one frontier bordered by *Salix* habitats, and forest margins on the other frontier (Figure 2). The main habitat types were the following: (a) Salix habitats. These ringed the main marshes adjoining the lakeside. Specimens of *C. rostrata*, decreased in abundance where the willow growths were more dense. Moss and *Carex* associations occurred in lowlying parts. (b) Sedge Meadows. These extended from *Salix* habitats to forest margin, but were isolated in other areas away from the main marshes. Hollows and pools abounded in these meadows and growths of *C. rostrata* or *C. atherodes* were dominant. (c) Forest margins normally were defined by the limit of waterlogged soil. Clumps of willows extended into the margins from sedge meadows. (d) Grassy forest clearings were isolated from the above habitats.

METHODS

The sampling program differed between years because of periodic flooding of habitats in 1969. Larvae and adults of *Patrobus* species were rare in comparison with some other marsh carabids and were mainly sampled by pitfall trapping. Various workers, particularly Greenslade (1964), and Southwood (1966), also Carter (1980) have pinpointed problems associated with data gathered by pitfall trapping of arthropods. In this study, I have restricted analyses to presence and absence data and to determining whether individuals of each species occurred at low or high levels of abundance in the same or different habitat types.

Patrobus populations were also sampled by hand collecting. These beetles were also collected from under cryptozoan boards (Cole, 1946) and were extracted by Tullgren funnels from quantitative soil samples brought back to the laboratory. For further details of the sampling program, see Carter (1971).

RESULTS AND DISCUSSION

Physical Differences Between Years

There were major differences in water levels and extent of waterlogged soil between 1968, on one hand, and 1969 and 1970, on the other hand. In 1968, melt waters from the winter snows had largely gone by mid-June and many hollows waterlogged in spring had dried out. Standing water had disappeared from transition habitats by mid-summer. By contrast, levels of marsh water in May 1969 were higher than at any time in the previous year. Heavy rains in July, August and September resulted in transition habitats becoming largely waterlogged and most hollows were flooded. Water levels remained high throughout 1970.

General Natural History of *Patrobus* Species

Data about seasonal activity and reproductive patterns of the four *Patrobus* species in various transition and marsh habitats are summarized in Figure 2 and Tables 1 and 2.

As noted previously by Lindroth (1961), North American *Patrobus* species overwinter as larvae and adults or as larvae only. At George Lake, only *P. lecontei* overwintered solely as larvae. Overwintered larvae of all species pupated in late June and July and gave rise to summer adults. Adults which had overwintered to a second year were known as spring adults. Both generations occurred together and could only be delimited during the period when summer adults were teneral with soft elytra.

Habitat Occupation

Ranges of spatial distribution of both larvae and adults of each species differed according to time of year. Ranges were greatest during the beetles' main periods of activity between May and September, and September and November for adults and larvae respectively (Carter, 1971). The ranges were least prior to and just after overwintering, the periods of low activity. During main periods of activity, individuals of *P. stygicus*, *P. lecontei* and *P. foveocollis* occurred mainly in different zones from forest clearings to lakeside, but there was overlap of all species in general habitat occupation (Figure 2). Larvae and adults of *P. lecontei* occupied mainly wetter parts of the transition zone, chiefly sedge meadows and *Salix* habitats, while individuals of *P. stygicus* ranged into deep marsh. Adults of *P. septentrionis* appeared to be as

hygrophilous as *P. lecontei* but were rare at George Lake and occurred chiefly in sedge meadows. Individuals of all four species were found in sedge meadows, and *Salix* habitats, but only *P. lecontei* and *P. stygicus* adults frequented large pools where there was little or no sedge growth.

In the dry year of 1968, larvae and adults of *P. foveocollis* predominated in drier parts of the transition zone, such as forest clearings, and were not associated with water. However, ranges of both stages of this species expanded radically in the wet years of 1969 and 1970. Both larvae and adults were widespread in all transition habitats, wet *Salix* habitats and pools in sedge meadows, and also in dry aspen-poplar habitats. High activity of larvae near the marshes in 1969 indicated that females oviposited there.

Habitat occupation of adults differed prior to and during periods of reproductive activity. Breeding spring adults of *P. stygicus* and summer adults of *P. lecontei* occupied the same general habitats in late June and July, namely pools in sedge meadows. *Salix* habitats, and (to a lesser extent) shallow marsh. In both years, summer adults and possibly spring adults of *P. stygicus* dispersed from these habitats into deep marsh in late July and August (Figure 2). It was not possible to compare data collected in 1968 with those in 1969 because of the different sampling programs in each year.

Data from mid-summer of 1969 (Table 3) were analyzed in tests of independence for which the G-test (Sokal and Rohlf, 1969) was employed, the distribution of which can be approximated by the X^2 distribution. Frequencies of adults of *P. stygicus* trapped in *Salix* habitats, shallow marsh and deep marsh varied according to time ($G=30.1$, $p < 0.005$). After July 25, activity in *Salix* habitats and shallow marsh decreased while that in deep marsh concomitantly increased. This was not so with *P. lecontei* adults ($G=5.9$, $p<0.1$) which were not trapped in deep marsh.

Range of spatial distribution of larvae and adults decreased as they dispersed to drier habitats such as *Salix*, banks of pools, and forest margin, prior to overwintering (Figure 2). No adults of *P. lecontei* were found to survive past their breeding season, but adults of the other three species tended to occur together in fall and winter. There were differences among late third instar larvae and pupae with respect to vertical distribution above and below soil surface. Larvae and pupae of *P. stygicus* were mainly in hummocks and bark above soil, while those of *P. lecontei* were found above and below soil. Despite intensive sampling, no larvae and pupae of *P. septentrionis* or no late third instar larvae and pupae of *P. foveocollis* and *P. septentrionis* were found. These stages of these two species probably occurred deeper in soil.

It is evident from the above data that different habitat associations of the *Patrobus* species at George Lake, particularly during their main periods of activity, were reflected mainly in horizontal distributions. Seasonal differences in habitat occupation have also been observed for adults of some marsh carabids in Britain. Dawson (1965) and Murdoch (1966) found clear differences in summer habitats between a number of congeneric marsh carabids, but observed that they overwintered together in drier habitats. It may be that adults of hygrophilous carabids normally aggregate in dry overwintering quarters, such as bark in forest margin, but disperse to different spring and summer habitats according to their respective responses to water. Thus congerneric carabids for example, such as those of the *Patrobus* species at George Lake, may come to occupy different habitats during their main breeding seasons.

Taxonomic Characters

A number of biologists (for example, Mayr, 1963 : 59ff.) have stressed the importance of studying physiological, behavioural, and ecological characters together with morphology. A number of ecological characters of the *Patrobus* species studied at George Lake (Tables 1 and 2) are here related to the classification and phylogeny of the group.

In a short-term study, such as this, it is difficult to delimit ecological characteristics of relevance to classification of a group of organisms, particularly when the study is confined to one part of the species' range. It is important to consider characters which are more general in nature and which are not likely to be affected markedly by environmental factors peculiar to any one area. Of the characters included in Table 1, period of reproductive activity, seasonal activity patterns of adults and larvae, and pupation sites are likely different in various parts of the species' range (for example, see Greenslade, 1965). Other characters such as overwintering stages, habitat occupation of adults and larvae, maximum length of adult life, and maximum age at which reproduction occurs are likely less affected. For instance, Lindroth's ecological notes (1961) indicate that habitats occupied, by *P. stygicus* and *P. lecontei*, in relation to water are uniform in much of their range.

In this study, observations were made over a wide range of weather conditions as differences were noted in habitat occupation, for example, between the dry year of 1968 and the wet years of 1969 and 1970. Thus, a better range of this ecological character was obtained. For instance, it appears that populations of *P. foveocollis* at George Lake are adapted to a wide spectrum of environmental conditions. This species is thought not to be associated with water (Lindroth, 1961), but the local distribution of populations in some other parts of the species range may expand and contract as they did at George Lake, according to weather changes between years.

Adults of *P. stygicus* are readily distinguished from those of *P. lecontei* by leg colour, features of prothorax, (see Figure 3), and male genitalia (Darlington, 1938; Lindroth, 1961). Likewise, the two species are distinguished by a number of ecological characters, including degree of hygrophily, age at which reproduction begins, maximum age at which reproduction occurs, and length of adult life (Table 2).

Patrobus longicornis Say frequents temperate environments in meadows, deciduous forests and arable land. It often occurs near the margins of lakes and rivers (Lindroth, 1961), but does not occur at George Lake. Features of habitat occupation of *P. stygicus* and *P. lecontei* (Table 1) indicate that these two species are more closely related to one another than either is to *P. longicornis* so also do morphological characters (Darlington, 1938).

The four *Patrobus* species at George Lake share a number of ecological characters. These include overwintering as larvae only or as larvae and adults, and overlap in general habitat preference (Tables 1 and 2). These and morphological characters, which Darlington (1938) Kühnelt (1941) and Lindroth (1961) described, indicate the close relationship of these species. Regarding stage(s) of overwintering, the majority of carabids of marshes and surrounding wet habitats of North America and Northern Europe overwinter as adults only (see Lindroth, 1949, 1963b, 1961-1969; Murdoch , 1967). The six North American *Patrobus* species (one of which, *P. septentrionis*, is holarctic) are exceptions, overwintering mainly as larvae or as larvae and adults (Lindroth 1961). At least two other species, the European *P. atrorufus* Stroem (see Thiele 1977) and *P. assimilis* Chaudoir (see Larsson 1939, Forsskåhl 1972) have similar overwintering stages.

Thiele (1977) noted that certain overwintering carabid larvae, including *Patrobus atrorufus* are active on the soil surface in late autumn and winter and are very cold hardy. The larvae of

P. stygicus, *P. lecontei* and *P. foveocollis* at George Lake are similar as they were very active at low temperatures (-2° to 5°C Carter, unpublished) in November. These were in contrast to *Patrobus septentrionis* larvae which were certainly subterranean. The condition of cold hardiness in larvae which overwinter would be advantageous to species living in boreal environments often with cold autumns preceding very cold winters. For instance, at George Lake, it allowed larvae of *P. stygicus* and *P. lecontei* to disperse from marsh habitats (in which during the late summer they hatched from eggs) to drier ones more suitable for overwintering.

PHYLOGENY

The following evolutionary interpretation of life history features and other ecological characters in based on Darlington's hypothesis of the phylogeny of the *Patrobus* species except that *Patrobus fossifrons* and *Patrobus stygicus* are regarded as distinct species rather than subspecies (see Lindroth, 1961). Darlington used morphological and zoogeographical characters. He wrote that the genus *Patrobus* probably originated in Asia and that the ancestors of the present day North American species migrated into the continent through the north at three times.

He proposed that the stock to arrive first divided into a boreal line (proto-*fossifrons-lecontei*) and a temperate line (proto-*longicornis*) which gave rise to *Patrobus longicornis*. The former stock "then divided into a western species (proto-*fossifrons*, probably west of the rockies) and an eastern species (proto-*lecontei*, probably east of the rockies)". Later proto-*fossifrons* entered the range of *P. lecontei* by migrating eastward. Eastern and western populations of proto-*fossifrons* became isolated and differentiated, giving rise to the ancestors of present day populations of *P. fossifrons* and *P. stygicus*. Darlington included these four species in the subgenus, *Neopatrobus*.

Morphological changes (for example, in the male genitalia, pronotum, leg size and colour) which took place during the evolution of the *Neopatrobus* group proceeded from a primitive extreme in *P. longicornis* to the derived extreme in *P. stygicus*. The series of characters can be described as a morphocline (Maslin, 1952).

The ecological trends of the ancestors of this first *Patrobus* stock that reached North America may be as follows. *Patrobus longicornis* frequents open habitats, mainly in temperate region(s) but appears not to be directly dependent on water (Lindroth 1961). This species appears to be the most primitive one of *Neopatrobus* (Darlington, 1938) and so the ancestors of this line may have frequented such habitats.

The *lecontei-fossifrons-stygicus* line diverged from temperate habitats into wet boreal ones, with the proto-*fossifrons-stygicus* stock becoming the more hygrophilous. The ancestors of *P. stygicus* probably dispersed into wetter habitats (marsh) than those frequented by the ancestors of *P. lecontei*. Today, at George Lake at least, this is reflected in the segregation of *P. stygicus* summer adults from *P. lecontei* adults during the breeding season.

These habitat associations can be described in terms of an ecocline. This cline proceeds from the primitive extreme in *P. longicornis* which does not occur in wet habitats to *P. lecontei* the largely transition zone dweller, at the borders of standing waters, to the derived extreme in *P. stygicus* which is a transition zone and marsh dweller and is found in standing waters. Thus, this ecocline extends from the primitive condition of least hygrophily to that of most hygrophily. It runs in the same direction as the morphoclines identified by Darlington (1938). The habitat preference ecocline is summarized in a phylogenetic diagram in Figure 3.

Patrobus foveocollis and *P. septentrionis* are presumed to have migrated to North America later than the *Neopatrobus* stock (Darlington, 1938), and *P. foveocollis* remained in drier boreal habitats than those entered by the *Neopatrobus* stock. The *Patrobus septentrionis* stock converged ecologically on species of *Neopatrobus* and invaded wet boreal habitats. Both *P. foveocollis* and *P. septentrionis* retained the primitive condition of overwintering as larvae and adults.

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Table 1. Habitat use and life history features of larvae and pupae of the four *Patrobus* species at George Lake

SPECIES	LARVAE				PUPAE	
	General habitats	Overwintering stage(s)	Main period of seasonal activity	Active on soil surface in Autumn	Pupation	Main sites
P. stygicus	Transition to deep marsh	Larvae, Adults	(1) July- ? (2) Sept.- Dec.	yes	late May- late June	Hummocks, bark in transition
P. lecontei	Transition and shallow marsh	Larva	late Sept.- early Nov.	yes	late May- late June	Soil, bark in transition
P. septentrionis	Transition	Larvae, Adults	late Sept.- ?	no	June	?
P. foveocollis	Transition also forest clearings	Larvae, Adults	Aug.- Nov.	yes	June	?

(1) refers to overwintered larvae
(2) refers to larvae of summer adults

Table 2. Habitat use and life history features of teneral adults and adults of the four Patrobus *species*

SPECIES	TENERAL ADULTS		ADULTS				
	Teneral emergence	Habitat	Adult Seasonal activity	Reproductive activity	Main oviposition sites	Age at which reproduction begins	Maximum age at which reproduction occurs
P. stygicus	late June - July	Transition	(1) May-? (2) mid-June-mid-Oct.	(1) late May-? (2) late July-mid-Aug.	*Carex* hummocks in marsh	1 month late July	2 - 12 months
P. lecontei	late June	Transition	mid-June-mid-Aug.	late June-mid-Aug.	*Carex* hummocks in transition	1 week (late June)	2 months
P. septentrionis	late June early July	Transition	early June-mid-Oct.	late July-mid-Aug.	?	?	?
P. foveocollis	late June	Transition	(1) early May-mid-Oct. (2) late June-mid-Oct.	(1) mid-May-late June	?	?	?

(1) refers to spring adults
(2) refers to summer adults

Table 3. Numbers of adullts of *Patrobus stygicus* and *P. lecontei* pitfall trapped in various habitats in mid-summer 1969

	Salix	*Shallow marsh*	*Deep marsh*
P. stygicus			
July 18 - 25	25	21	21
July 25 - Aug. 3	12	4	48
	37	25	69
P. lecontei			
July 18 - 25	52	15	0
July 25 - Aug. 3	27	21	
	79	36	0

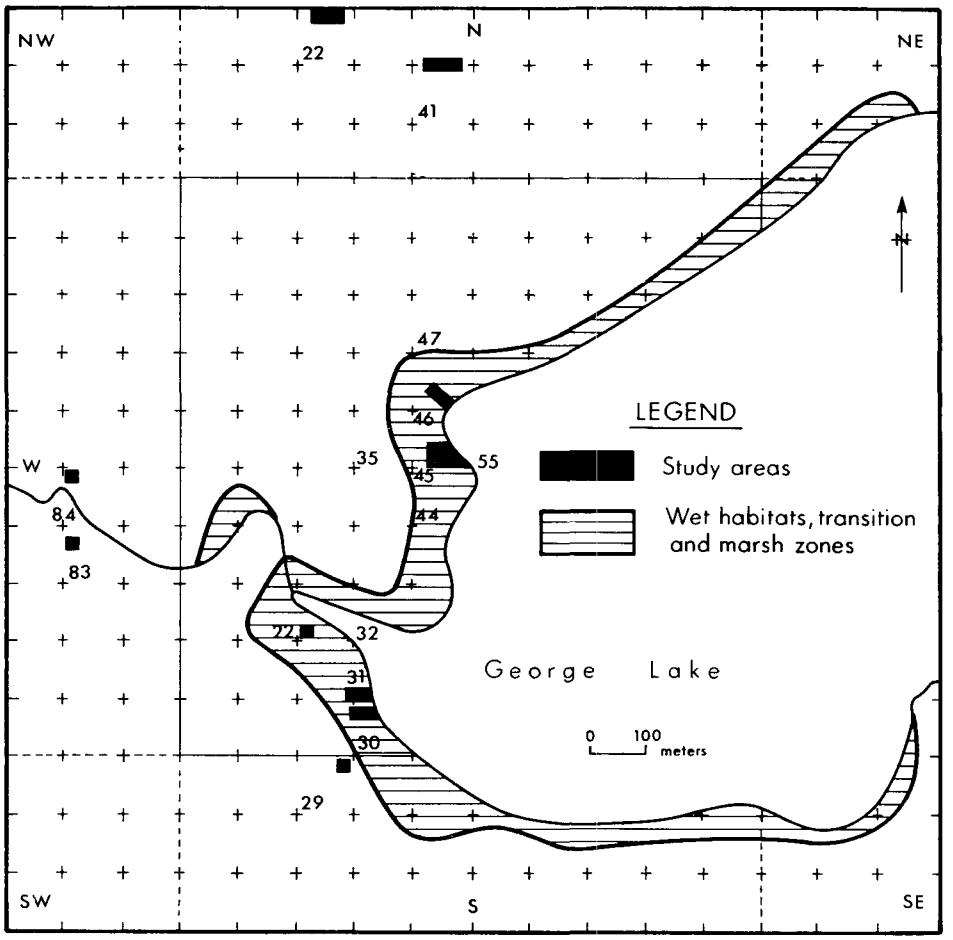

Figure 1. George Lake field station showing wet habitats and study areas. The station numbers of study areas were designated by the grid reference of the S.W. corner of the quadrant(s) in which each occurred. The habitats in which the study areas occurred and their station numbers were: adjoining the lake, main marsh, *Salix* and pools in sedge meadows (30, 31, 45 and 46); forest margin (29S), grassy forest clearings (83W and 84W); small marsh (22N) and sedge meadows (22, 41N).

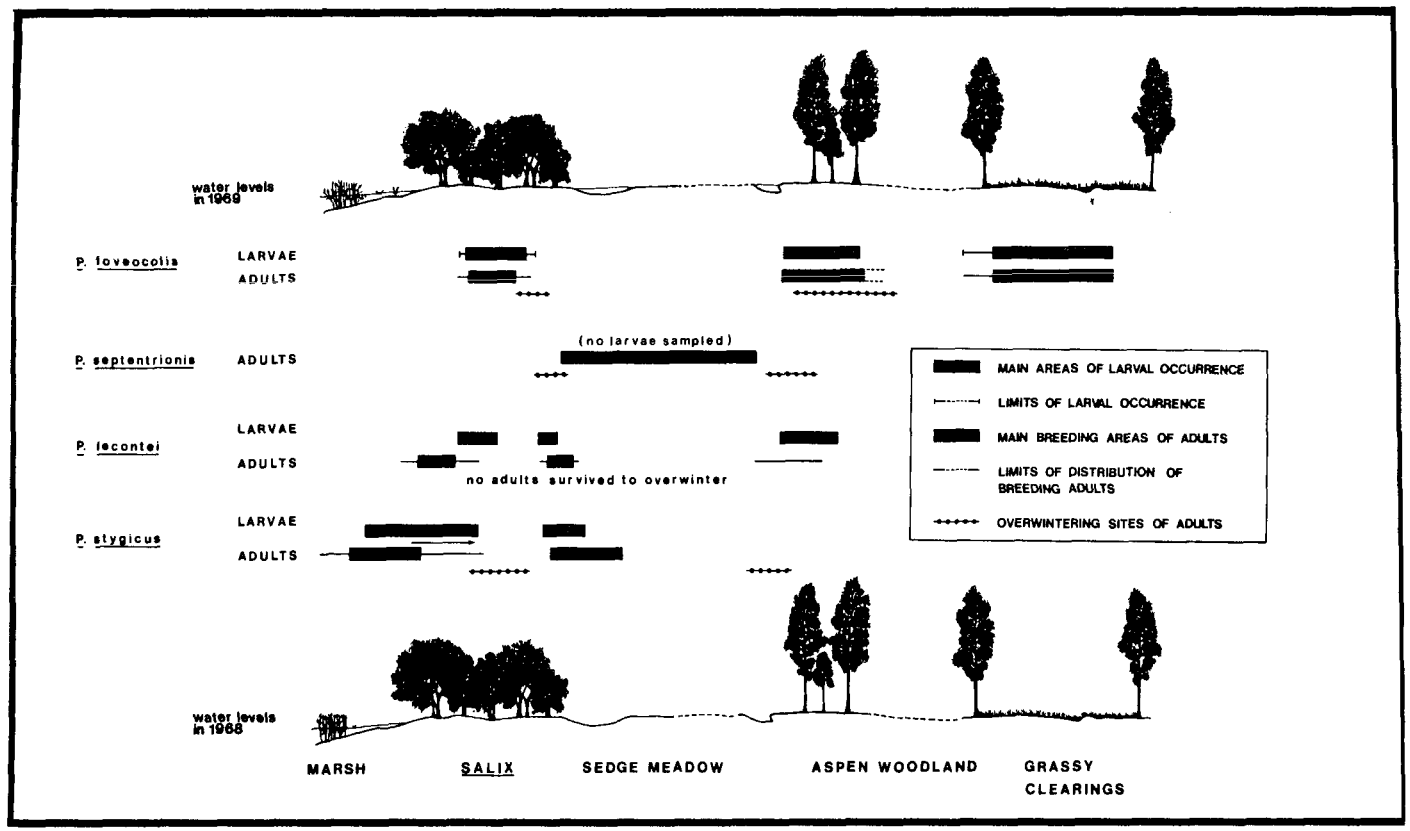

Figure 2. Occurrence of larvae and adults of *Patrobus* species in wet habitats at George Lake.

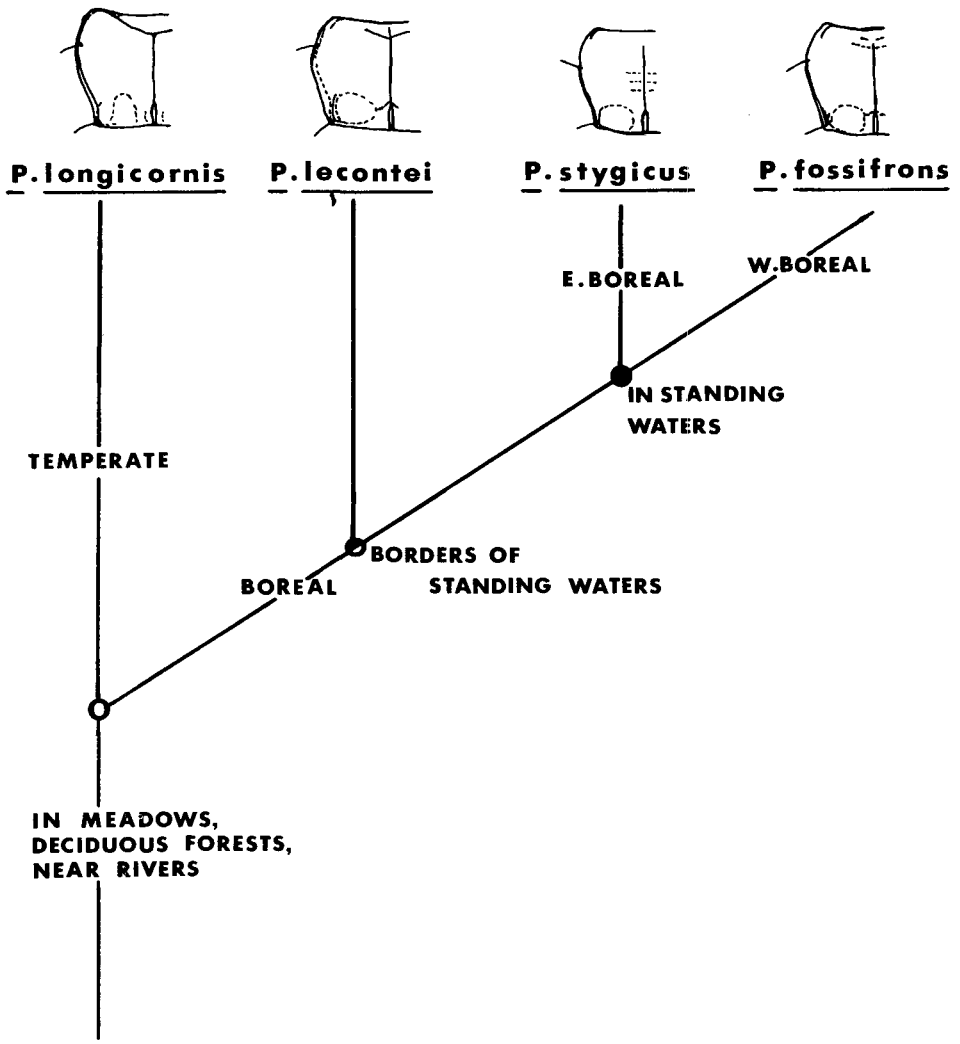

Figure 3. Diagram of the possible phylogeny of the North American *Patrobus (Neopatrobus)* species, after Darlington (1938). A summary of the geographical distributions and habitat preferences of these species is included.