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PERSISTENCE OF *BRANCHINECTA PALUDOSA* (ANOSTRACA) IN SOUTHERN WYOMING, WITH NOTES ON ZOOGEOGRAPHY

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ABSTRACT

The fairy shrimp *Branchinecta paludosa* is a persistent resident of aestival ponds at high elevation in the Medicine Bow Mountains of southern Wyoming. These populations are far removed from the Arctic tundra habitat that typifies the distribution of the species, and appear to represent the southern margin of the range in North America. All of the records for the northern United States and southern Canada appear to lie along the Central Flyway that is a major migration route for waterfowl and shorebirds that nest in the Arctic. Passive dispersal probably provides for frequent colonization of marginal habitats and gene flow to established populations.

The fairy shrimp *Branchinecta paludosa* (Müller) is widely distributed in the circumpolar tundra of the Holarctic region (Vekhoff, 1990). In Europe, it occurs chiefly at latitudes above 60°N, but there are isolated records from the High Tatra Mountains on the border between Czechoslovakia and Poland at about 49°N (Brtek, 1976). Records for Russia are typically along the Arctic margin, but include the southern tip of the Kamchatka Peninsula at 52°N (Linder, 1932). In North America, it is found in Alaska and most of the provinces of Canada (Linder, 1932; Reed, 1963; Belk, 1975; Daborn, 1978). There are also a few scattered records from the contiguous states of the United States (Linder, 1941; Lynch, 1958; Belk, 1977; Saunders, 1981a). The occasional southern record notwithstanding, most known populations occur near the Arctic Ocean.

Recent collections of *B. paludosa* from the Medicine Bow Mountains of southern Wyoming suggest that the species is both locally common and temporally persistent. *Branchinecta paludosa* was collected from eight ponds in the Snowy Range in Albany County, Wyoming (R79W, T16N, sections 9, 10, 15, 16 on USGS 7.5 minute series Medicine Bow Peak Quadrangle). This species has been collected consistently since 1987 in conjunction with studies at the Glacier Lake Ecosystem Experiment Site (GLEES). These ponds are best characterized as aestival habitats (Eng *et al.*, 1990; Daborn and Clifford, 1974) because they always contain water but may freeze to the bottom in winter. Specimens from two sites have been deposited in the University of Colorado Museum (UCM 2192, 2193, 2194). The Snowy Range is an axial remnant which rises about 300 m above the surrounding Medicine Bow Mountains (Houston and others, 1978). The ponds are mainly in the upper Telephone Creek drainage at elevations of 3,200–3,350 m. Most of the ponds are underlain by the Nash Fork formation (Houston and others, 1978), and the characteristic metadolomite is present in all but one of the ponds. The ponds support no fish and most tend to be low in ionic content (Table 1).

Prior to our collections, *B. paludosa* had been reported twice from the Medicine Bow Mountains (Linder, 1941; Horne, 1967). Linder's report is very likely from the same general area as the present records. The sample (USNM 78574) was collected by Irving H. Blake on 4 July 1935 from the Medicine Bow Mountains, and contains rather cryptic locality data: "G.C. no. 303–3 (10) a. ch. Sta. E. Temporary pond. alt. 9,700 ft." Although the 9,700 ft (2,957 m) contour traverses considerable territory in the Medicine Bow Mountains, the possible locations are drastically reduced by examining intersections of that contour with roads that existed in 1935. The most likely prospect is Wyoming Highway 130 that skirts the Green Rock Campground (now a picnic area) which bears the United States Forest Service identification number 303. A small temporary pond exists near the picnic area on the south side of the Nash Fork at an elevation of approximately 3,000 m (R79W, T16N, section 13 on USGS 7.5 minute series Centen-

Table 1. Major ion chemistry of three ponds inhabited by *Branchinecta paludosa* in the Medicine Bow Mountains, Wyoming.

	Pond near Lost Lake 17 June 1991	Pond near Towner Lake Road 08 June 1991	Pond sampled by Horne (1967)
pH	6.1	7.0	7.0
Ca, mg/l	0.8	2.8	2.0
Mg, mg/l	0.2	0.7	3.0
Na, mg/l	0.2	0.2	1.0
K, mg/l	0.2	0.5	0.0
Cl, mg/l	0.2	0.2	3.0
SO_4, mg/l	0.9	0.5	2.0
HCO_3, mg/l	2.2	12.0	4.0
Conductance, μmho/cm	9.6	29.0	35.0

nial Quadrangle). At the time the pond was located in early August 1991, it was nearly dry, but yielded one specimen of *B. paludosa*. This pond remains the most likely match for Blake's locality despite a small discrepancy in elevation.

Horne (1967) reported that *B. paludosa* occurred in alpine ponds in the Medicine Bow Mountains, but gave no specific locality data. On the basis of elevation alone (3,000–3,500 m), the pond must be very close to the ones that we sampled. Furthermore, the chemistry is similar (Table 1). Horne recalls collecting *B. paludosa* from a pond in the upper Telephone Creek drainage as well as from a relatively large lake (Bellamy, Marie, or Mirror) in the nearby South French Creek drainage (Francis Horne, personal communication to Denton Belk, 30 September 1991). The lakes in the South French Creek drainage are now stocked with trout and contain no fairy shrimps.

Several unpublished collections add support to the view that *B. paludosa* is common in the Medicine Bow Mountains and the populations persist over time (Table 2).

The zoogeographical significance of the Wyoming records is greater than recognized previously. The Colorado-Wyoming border is probably the southern extent of the North American distribution of *B. paludosa*. A previous record of *B. paludosa* from the Kaibab Plateau in Arizona (Belk, 1977) has proven to be a misidentification. A description of what is now known to be a new species of *Branchinecta* is in preparation (M. Fugate and D. Belk). There is also a previous record for a site near Salt Lake City, Utah (Maynard, 1976), but the validity of the report has not been confirmed despite efforts by Belk to locate voucher specimens. Salt Lake City lies just south of the latitude that separates Colorado and Wyoming. Confirmed records published for the contiguous United States are thus restricted to Irish Canyon of extreme northwestern Colorado (Saunders, 1981a), the plains of north central Montana (Lynch, 1958), and the Medicine Bow Mountains of southern Wyoming (Linder, 1941). Lynch's specimens from Montana are in an uncataloged collection in the USNM (Acc. No. 294523).

The record of *B. paludosa* from northwestern Colorado is very close to the Wyoming border and thus is little different in latitude from the Wyoming collections, albeit at a lower elevation. The ability of this population to inhabit the same pond from year to year is not known, because no subsequent attempts have been made to sample this ephemeral pond. The same area was sampled by Powell's survey many years ago, but *B. paludosa* was not reported (cf. Packard, 1883; Saunders, 1981b). G. D. Langstaff collected *B. paludosa* from seven sites in the vicinity of the Great Divide Basin, Wyoming (now in D. Belk's personal collection); these sites are about 240 km north of Irish Lakes.

The Medicine Bow Mountains are

Table 2. Unpublished distribution records for *Branchinecta paludosa* in the Medicine Bow Mountains of southeastern Wyoming.

Locality data	Collector	Status
Pond near Big Brooklyn Lake, Albany County, 24 August 1952	J. E. Lynch	USNM Acc. 294523
NE side of road several miles west of University of Wyoming Science Summer Camp, 8 August 1967	J. E. Lynch	USNM Acc. 294523
>40 miles west of Laramie	J. E. Lynch	USNM Acc. 294523
"Jon's Pond," 10,670 ft., 3.5 km NE of Snowy Range Pass, 3 September 1989	G. Langstaff	D. Belk, personal collection

thousands of kilometers from the Arctic tundra habitat that is typical for *B. paludosa*. Nevertheless, the temporal persistence of these populations argues that southern Wyoming is a stable part of the range for the species. The southern limit for *B. paludosa* in North America is at a lower latitude than the limit in Europe (41° versus 49°). Brtek (1976) considered the permanent populations in Central Europe to be typical glacial relicts. By analogy it could be inferred that the southern limit in North America is defined by relict populations. Indeed, Belk (1977) once speculated that the populations in Utah and Arizona were Pleistocene glacial relicts. The distribution of *B. paludosa* for North America differs substantially from that recorded for Europe in terms of the degree to which the southern fringe is isolated from the Arctic tundra populations. The Tatra populations are apparently quite isolated; whereas, the Wyoming populations represent the terminus of a chain of records extending through Montana and Alberta (Lynch, 1958; Hartland-Rowe, 1965; Anderson, 1974; Daborn, 1978). The presence of populations between Wyoming and the Arctic diminishes the likelihood that the Wyoming populations are glacial relicts.

Donald (1983) studied anostracans in a temporary pond near Calgary, Alberta, for 14 consecutive years and found that *B. paludosa* was not present in all years. He concluded that the observed pattern might be explained by extinction and recolonization, or by a combination of long-term egg viability and specific physiological requirements that were not always met. Daborn (1978) also believed that intermittent reintroduction was probably important for the maintenance of populations of *B. paludosa* in Alberta.

The frequency of colonization is clearly important for populations subject to extinction. For example, Johansen (1921) reported an isolated population near Montreal, Canada (45.5°N), that was collected once and failed to appear in subsequent years. He speculated that the founding of this population was a chance colonization event soon followed by extinction.

Among the various potential agents of passive dispersal, waterfowl and shore birds are the most likely to be of significance for the distribution of *B. paludosa* (Daborn, 1978; Anderson, 1971). Most of the ponds in question lie along the western edge of the Central Flyway which is a major migratory route for birds that nest in the Arctic and winter much farther south (Fig. 1). The major routes displayed in Fig. 1 were derived chiefly from the movements of waterfowl (Lincoln, 1939). Links to Bear Lake and Great Salt Lake in Utah are especially interesting in relation to those Colorado and Wyoming records that are west of the Continental Divide. These links also hint at validity for the Utah record of Maynard (1976).

It is well known that waterfowl can serve as agents of passive dispersal for the eggs of various crustaceans, including anostracans (e.g., Malone, 1965; Proctor, 1964; Proctor *et al.*, 1967). Colonization by *B. paludosa* could proceed in small jumps as disseminules of successful colonists are carried farther and farther from the Arctic by successive migrations along the Central Flyway. The geographically narrow pattern of distribution in southern Canada and the northern United States is consistent with passive dispersal along the flyway, and the stochastic nature of extinction and recolonization could explain the erratic temporal persistence of populations in Alberta.

It is thought that disjunct distributions for two other Arctic anostracans are also the result of passive dispersal. *Artemiopsis stefanssoni* and *Polyartemiella hazeni* have been recorded from southern Alberta (Hartland-Rowe and Anderson, 1968; Daborn, 1976, 1977). Both sites are along the Central Flyway.

The Central Flyway does not terminate in Wyoming, however. Birds migrate much farther south to reach winter habitats, but the range of *B. paludosa* does not extend farther south. The apparent absence of *B. paludosa* in adjacent high mountain areas is puzzling. Physical habitat conditions in the Rocky Mountains of Colorado cannot be vastly different from those in southern Wyoming, and the chemistry of the ponds appears to differ little from that found at high elevation in the Colorado Front Range (cf. Saunders and Kling, 1990). Furthermore, migration routes cross the Colorado Rockies in two places (Fig. 1). Nevertheless, high elevation sites in Colorado almost invariably contain *B. coloradensis* (Saunders,

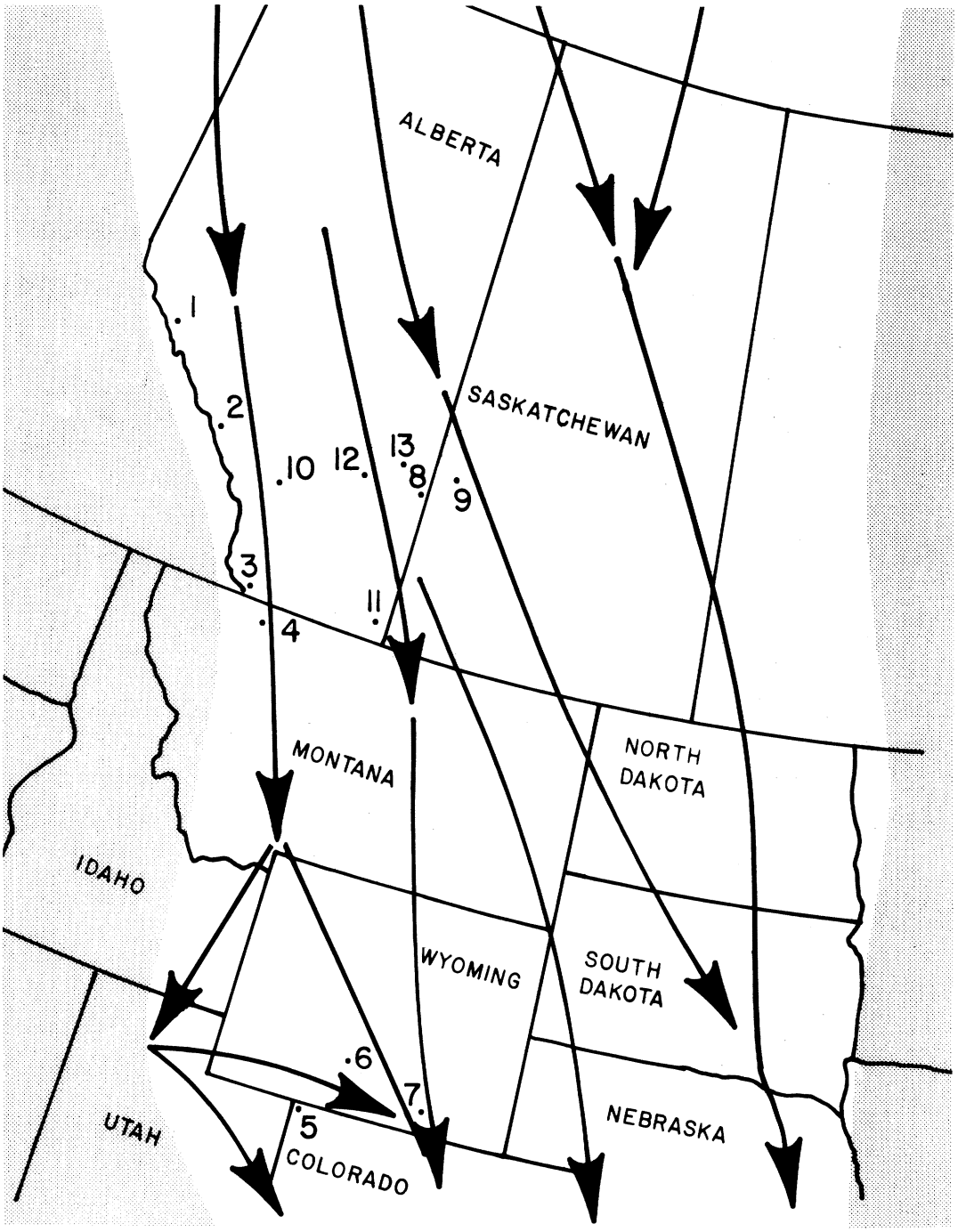

Fig. 1. Distribution of *Branchinecta paludosa* in southern Canada and northern United States. The gray border defines the boundary of the Central Flyway. Arrows within the flyway represent major migration routes as described by Lincoln (1939). 1—Anderson, 1974; 7 sites in Jasper National Park, Alberta. 2—Anderson, 1974; 8 sites in or near Banff National Park, Alberta. 3—Anderson, 1974; 2 sites in Waterton Lakes National Park, Alberta. 4—Lynch, 1958; 2 sites near Browning, Montana. 5—Saunders, 1981a; Irish Canyon, Colorado. 6—Belk collection; 7 sites in Great Divide Basin, Wyoming. 7—Present study; Linder, 1941; Horne, 1967; at least 10 sites in the Medicine Bow Mountains, Wyoming. 8—Daborn, 1978; 2 sites, Alberta. 9—Hartland-Rowe, 1965; 4 sites near Kerrobert, Saskatchewan. 10—Hartland-Rowe, 1965; 3 sites in and near Calgary. Donald, 1983; 1 site in Calgary. 11—Hartland-Rowe, 1965; 2 sites, Alberta. 12—Hartland-Rowe, 1965; 2 sites near Hanna, Alberta. 13—Hartland-Rowe, 1965; 1 site near Consort, Alberta.

1981a). The relationship between *B. coloradensis* and *B. paludosa* is made more intriguing by the occurrence of both species in the Medicine Bow Mountains. Lynch (1958 and USNM Acc. No. 294523) reported *B. coloradensis* from ponds in the same drainages where *B. paludosa* occurs. The absence of cooccurrences of these two species, which can inhabit adjacent ponds in the Medicine Bow Mountains, points to a potentially interesting area of study. Competition may well be an important factor. The ranges for *B. paludosa* and *B. coloradensis* overlap extensively north of Colorado, but apparently it is very unusual to find both species in the same pond. It remains a mystery as to what factor or factors will tip the balance to one species or the other.

Branchinecta paludosa has been recorded in the Medicine Bow Mountains for over 50 years and appears to be a very persistent resident of ponds in the Snowy Range. Despite the temporal persistence and geographical extremity of these populations, it is problematic that they are glacial relicts. The opportunity for passive dispersal from more northern sites along the Central Flyway provides for gene flow where a population already occurs or colonization where one does not.

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