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CLIMBING ADAPTATIONS IN THE HINDLIMB MUSCULATURE OF THE WOODCREEPERS (DENDROCOLAPTINAE)¹

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Key words: Adaptation; Dendrocolaptinae; hindlimb muscles; woodcreepers.

The woodcreepers (Furnariidae: Dendrocolaptinae) climb vertical tree trunks suspended by their forward toes and supported by their stiffened tails. They are one of several groups that independently evolved such scansorial behavior (Richardson 1942, Bock and Miller 1959, Storer 1971). This paper is part of a wider study of the woodcreepers (Raikow 1993, 1994; Raikow et al. 1993; Bledsoe et al. 1993) and its purpose is to consider whether the hindlimb muscles of the woodcreepers show structural adaptations for scansorial behavior.

Stolpe (1932) suggested that when birds assume perching or standing postures the center of gravity lies vertically above the hindlimbs, and gravity tends to flex the leg joints; this is counteracted by the postural activity of the extensor muscles of the legs. In a bird that is clinging vertically, however, the center of gravity is displaced horizontally relative to the substrate. The bird is anchored to the tree by flexion of the forward toes, whose claws penetrate the bark, and its tendency to fall extends the leg joints, and is resisted by the flexor muscles. Thus, in the evolution of scansorial behavior a functional reversal occurs as a major postural role is transferred from the extensor muscles to the flexors. Moreno (1991) analyzed climbing adaptations in treecreepers (*Certhia* spp.), and reiterated the idea, based on Stolpe (1932), Spring (1965), Winkler and Bock (1976), and Norberg (1986), that it is advantageous for a tail-braced bird to minimize the distance from its

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center of gravity to the tree trunk. Moreno (1991) suggested, furthermore, that certain modifications in *Certhia* constitute climbing adaptations because they strengthen the hindlimb flexor muscles and reduce the extensors, changes that facilitate the abovementioned postural advantage.

The adaptive value of muscle enlargement in association with increased function is of obvious significance. The value of reduction, in contrast, is less obvious. It may be associated with energy savings in the development and maintenance of the muscles. In addition, reduced size of one muscle may make space available for the enlargement of other muscles. Adaptive changes in the evolution of muscles appear to be related to the idea that, other things being equal, the maximum strength of contraction is proportional to muscle mass. Of course, other things are seldom equal. Many factors contribute to muscle function, including fiber arrangement, fiber type, number of joints crossed, and the synergistic actions of muscle groups. These factors are not considered herein, and so this study provides only a first approximation of functional evolution in muscles. Nevertheless, the differences reviewed are distinct and correlate well with behavior, suggesting that the analysis is valid.

The term *adaptation* has several meanings in biology. It may refer to a physiological adjustment, or to a process of becoming adapted in an evolutionary sense. The meaning intended here, however, is of a character that is suited to some purpose. The definition of this meaning of adaptation has itself evolved (Burian 1992, West-Eberhard 1992). Lauder et al. (1993) give a recent formulation based on Baum and Larson (1991), which may be paraphrased as follows: *An adaptation is a feature with current utility, which increases the fitness of the organisms that possess it, and which has evolved under natural selection for its current function.* This concept has two components; adaptation as a state-of-being (utility) and as a product of history (evolution). Some workers exclude the latter component from their definition of an adaptation (Reeve and Sherman 1993). Gould and Lewontin (1979) emphasized that not all features of an organism are adaptations. The suggestion that a feature is an adaptation is a hypothesis subject to testing. I will evaluate the adaptive nature of several myological innovations in the woodcreepers by testing their conformity with the two components of the above definition of an adaptation.

MATERIALS AND METHODS

The myological analysis in this paper is based on previously published descriptions and illustrations of the hindlimb muscles in 42 species of woodcreepers, including representatives of all 13 genera (Raikow 1993), as well as analyses of intra- and interspecific variation in muscular anatomy (Bledsoe et al. 1993, Raikow et al. 1993). I examined derived states in the muscles (Raikow 1993) to see how each was related to the hypothesis that in scansorial birds the flexors are strengthened and the extensors diminished. I found several changes that were consistent with this idea (discussed below), some that were irrelevant to it, and none that were contradictory.

The phylogenetic framework for the present study is

based on a cladistic analysis of 36 characters with 49 transformations from the hindlimb muscles, bill, nostrils, feet, and tail in the same 42 species of woodcreepers. The analysis was done by computer using the PAUP program, version 3.0s (Swofford 1991), a heuristic search method, and the accelerated transformation method of character optimization (Raikow 1994). A review of avian hindlimb muscle function is given in Raikow (1985: 93–111).

RESULTS

M. iliotibialis cranialis. This is the main flexor (protractor) of the thigh (See Raikow 1993, Fig. 2). It passes from the cranial end of the pelvic girdle and adjacent vertebrae to insert on the head of the tibiotarsus. In woodcreepers the muscle is wider than in most passerines, and extends its insertion onto the surface of *M. femorotibialis internus*, which lies on the medial surface of the thigh; this augments flexion of the thigh. The same condition occurs in many ovenbirds (Furnariinae; Raikow, unpubl. observ.), which suggests that it is not an innovation of the woodcreepers *per se*. The significance that this character distribution has for addressing adaptation status will be discussed below.

M. pubo-ischio-femorialis. The main thigh extensor is *M. pubo-ischio-femorialis*, which has two separate bellies. In woodcreepers the cranial belly is unremarkable, but the caudal belly is reduced in both width and length. This reduction in size is often quite dramatic, the muscle in most woodcreepers being little more than a vestige. The functional consequence of this change is a weakening of femoral extension (see Raikow 1993, Fig. 10).

M. iliotibialis lateralis. An extensor of the thigh, *M. iliotibialis lateralis* pars postacetabularis undergoes reduction in some woodcreepers, along either its cranial or its caudal margin (Raikow 1993, Fig. 1). Either case weakens femoral extension.

M. flexor cruris lateralis. This large thigh muscle shifts its main area of insertion distad across the knee joint from the femur to the tibiotarsus (Raikow 1993, Figs. 5–7), thereby augmenting the strength of tibial flexion at the expense of femoral extension. This occurs in most furnariines, except terrestrial species, which suggests that it may be of general significance to arboreal birds. Except for *Drymornis*, however, this effect is increased in woodcreepers by further development of the tibial lobe of pars pelvica (Raikow 1993, Figs. 6, 7).

M. gastrocnemius. Tarsal extension is weakened because *M. gastrocnemius*, the main extensor, shows reduction in two of its three bellies. Pars intermedia is distinctly truncated in most woodcreepers (Raikow 1993, Fig. 15), and pars medialis is narrowed in some (Raikow 1993, Fig. 16).

Mm. flexor hallucis longus and flexor digitorum longus. A distinctive characteristic of the woodcreepers is the relationship between *Mm. flexor hallucis longus* (FHL) and *flexor digitorum longus* (FDL) (Raikow 1993, Figs. 18, 19). In most passerines these muscles have largely separate origins, but in woodcreepers they are intermingled in a unique way. FDL has acquired a large femoral head that adds considerably to its contractile strength. This is not unique in passerines, but what is

distinctive is how it has interacted with the overlying FHL. The usually fleshy origins of FHL have been reduced to tendons, unlike the condition in other forms, including furnariines. The space once occupied by the fleshy origin of FHL now holds the femoral head of FDL. Thus while FDL has increased in mass, FHL has decreased. Woodcreepers are supported by the forward toes, which are flexed by FDL, but not by the hallux, which is flexed by FHL. Thus it appears that the strength of the deep plantar muscles in woodcreepers has been reapportioned in a manner more effective for climbing.

Ossified tendons. Woodcreepers are unusual among passerine birds in that the tendons of insertion of most of the crural muscles are ossified. This condition may be functionally correlated with the physical stresses resulting from climbing. It is discussed elsewhere (Bledsoe et al. 1993; Raikow 1993).

DISCUSSION

The woodcreepers show a pattern of evolutionary changes that result in a strengthening of the hindlimb flexor muscles and a weakening of the extensors. This pattern parallels that reported by Moreno (1991) in the Certhiidae, which supports the idea that these changes are adaptive for climbing. However, the specific changes in the various muscles are not the same in the two groups, so a functionally similar result has been achieved in different ways.

To test whether these changes constitute adaptations, I will consider whether they agree with the definition of adaptation given above, including criteria both of utility and of evolutionary history. As to utility, the suggestion that the changes are climbing adaptations is biomechanically consistent with the postures of scansorial birds, and it is plausible that an improvement in an important behavior will enhance fitness. That most of these features have evolved for their current usage is suggested by their correlation with scansorial behavior and their evolutionary origins at various nodes of a phylogenetic tree (Raikow 1994). Thus, they constitute synapomorphies of clades for which they are hypothesized to be adaptations (Raikow 1988). The idea that they evolved under selection is testable by method III of Endler (1986), which would suggest that functional convergence in "unrelated" groups (scansoriality evolved separately in the Certhiidae and Dendrocolaptinae) indicates that convergent features in the two groups evolved under natural selection. Some of the changes are synapomorphic for all woodcreepers, and are postulated to be adaptations for the scansorial habit that accompanied the origin of the group. Other changes (see character descriptions above and Raikow 1994) are synapomorphic for subgroups of woodcreepers, and presumably constitute adaptive refinements that improve the efficiency of climbing in those clades.

One muscle, *M. iliotibialis cranialis*, requires additional consideration. The derived state occurs both in woodcreepers and in many furnariines. It is probable that the Dendrocolaptinae and the furnariine species form a clade (Raikow 1994), and it is therefore possible that the derived state arose before the origin of the woodcreepers. In that case its original functional significance would probably not be in relation to scansoriality. It may have arisen as an adaptation for more

general arboreal agility, subsequently proving useful in the specific movements and postures of vertical climbing. In this case, at least under a historical definition of adaptation, its presence in woodcreepers would constitute, in the terminology of Gould and Vrba (1982), an exaptation rather than an adaptation.

CONCLUSIONS

Derived character states of the hindlimb muscles of woodcreepers (Dendrocolaptinae) collectively strengthen flexion and weaken extension of the limb. This pattern parallels that evolved independently in the Certhiidae (Moreno 1991), but was accomplished by different myological modifications. That the sets of changes in each group have the same functional effect and are also correlated with scansoriality suggests both that they are adaptations and that they evolved independently under natural selection.

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SURVIVAL ESTIMATES FOR SNOWY PLOVERS BREEDING AT GREAT SALT LAKE, UTAH¹

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Key words: *Charadrius alexandrinus*; Great Salt Lake; mark-recapture study; resighting probability; Snowy Plover; survival estimates.

Current knowledge of the breeding biology of Snowy Plovers (*Charadrius alexandrinus*) in North America is primarily confined to studies of their reproductive success (Boyd 1972; Page et al. 1983, 1985; Paton and Edwards 1990; Paton 1994), mating system (Boyd 1972; Warriner et al. 1986), dispersal (Stenzel et al., in press), and distribution (Page et al. 1991). Snowy Plover populations breeding along the Pacific Coast were recently listed as threatened by the U.S. Fish and Wildlife Service in April 1993 (Federal Register 1992), yet there are no quantitative survival estimates available for this species.

Page et al. (1983) and Warriner et al. (1986) calculated minimum annual survival estimates of 0.743 and 0.752, respectively, based on the subsequent resightings of banded adult Snowy Plovers in coastal California. However, those rates probably underestimated actual annual survival rates because they were not based on capture-recapture models, such as a Jolly-Seber

modeling approach (Jolly 1965, Seber 1965). Jolly-Seber models use resightings to estimate survival probabilities for birds that were not resighted but were actually still alive. The purpose of this paper is to determine annual survival estimates for Snowy Plovers at Great Salt Lake, Utah, using a hierarchical modeling approach recently developed by Lebreton et al. (1992).

METHODS

The study was conducted at eight sites at Great Salt Lake, Utah, from 1990 to 1993: Locomotive Springs Waterfowl Management Area (WMA) (41°41'N, 112°55'W); Harold Crane WMA (41°20'N, 112°08'W); the West Warren area of Harold Crane WMA (41°18'N, 112°08'W); the northwest corner of Ogden Bay WMA (41°14'N, 112°14'W); Howard Slough WMA (41°09'N, 112°09'W); West Layton Marsh (41°02'N, 112°05'W); Farmington Bay WMA (40°55'N, 111°55'W) and 2 km northeast of Saltair Beach (40°46'N, 112°08'W) (Paton 1994). Fieldwork was centered at two focal sites, Howard Slough WMA and West Layton marsh. Focal sites were surveyed 2–3 times per week from 1 April to 31 August, with one observer in 1990 and two observers from 1991 to 1993. The other six sites were visited 1–4 times per month.

Incubating birds were trapped with a circular funnel trap (Lessells 1984); others were captured 0.1–1 km

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