Short communications

Sexual bill dimorphism supports separation of the woodpecker genera *Dendrocopos* Koch (1816) in the Palaearctic and *Picoides* Lacépède (1799) in the Nearctic

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Woodpeckers have long been recognized as a monophyletic taxon, a decision that has never been seriously disputed (Sibley & Ahlquist 1990, Webb & Moore 2005, Benz *et al*. 2006). However, morphological studies of their intrageneric relationships have given different conclusions. Based primarily on anatomy, Ridgway (1914), Burt (1930), Peters (1948) and Goodge (1972) gave one classification scheme, whereas Goodwin (1968) and Short (1982), based mostly on plumage characters and geographical distributions, gave another. Phylogenetic studies with molecular character sets have conflicted with these classifications (e.g. DeFilippis & Moore 2000, Prychitko & Moore 2000, Weibel & Moore 2005) and also suggested that plumage convergence among woodpeckers has probably caused numerous classification errors.

The most recent taxonomic revision of the woodpeckers was given by Short (1982) who believed that highly similar plumage is a good indicator of common ancestry and very unlikely to have arisen by convergence. The true woodpeckers, Picinae, comprise approximately 218 species in 23 genera (*sensu* Short). The species in two of these genera, *Dendrocopos* and *Picoides*, move and behave like typical arboreal woodpeckers, and are often referred to as «pied woodpeckers» because of their black-and-white plumage. Mainly based on physical characters, including body size and plumage pattern, as well as behavioural traits such as feeding habits, Short (1971, 1982) and Winkler *et al*. (1995) retained *Dendrocopos* in *Picoides*, whereas Ouellett (1977), Sibley & Monroe (1990) and del Hoyo *et al*. (2002) classified *Picoides* (*sensu* Short) in the Nearctic (North America) but separated the genera *Dendrocopos* and *Picoides* in the Palaearctic (mainly Europe).

Although phylogenetic results from the past decade differ from Short's taxonomic scheme (e.g. Weibel & Moore 2002a, b, Webb & Moore 2005), Short's classification is still used by American authors. In Europe, however, several authors separate the genera *Dendrocopos* and *Picoides* (e.g. del Hoyo *et al*. 2002). As no clear link has been established between the relationships of Old World and New World species of *Picoides* (*sensu* Short), the genus is in need of systematic revision (Weibel & Moore 2002a, Fuchs *et al*. 2007).

As the recent phylogenetic studies were mostly limited to the Americas, and few Eurasian woodpeckers have been analysed, the generic

relationships of *Dendrocopos* in the Palaearctic and *Picoides* (*sensu* Short) in the Nearctic are still poorly known. Fuchs *et al*. (2007), however, considered *Dendrocopos* to be paraphyletic and *Picoides* polyphyletic. In the present paper, I have selected a series of reproductive patterns and sexual bill dimorphism, which are considered to be of significance, in an attempt to find out whether the Nearctic members of the genus *Picoides* (*sensu* Short) differ from the Palaearctic members of the genus *Dendrocopos*.

METHODS

The data were mainly extracted from Cramp (1985), Winkler *et al*. (1995), del Hoyo *et al*. (2002) and The Birds of North America (1994-2002). For each species, the following mean values were noted: length of the bird (cm), female body mass (g), bill length (culmen to base, mm), egg weight (g), egg volume index (length x breadth^2/1000), relative egg volume (egg volume index divided by female body mass), incubation period (d), nestling period (d), total nesting period (incubation + nestling periods), bill dimorphism (ratio of mean male to female bill length). For all these variables, I have used the midpoint of the range of values of the nominate subspecies. The body mass of females is used when this datum is available; otherwise the body mass of the species is used. Since information about some species is scanty or even lacking, sample sizes inevitably vary. Of the 22 *Dendrocopos* species found in the Old World, five live in Europe, and of the 12 *Picoides* species (*sensu* Short), nine live in North America.

All tests are two-tailed. Means are presented ± 1 SD. Nonparametric Spearman rank tests are used for pairwise correlations.

RESULTS

Body mass, reproductive patterns and sexual bill dimorphism

Although the mean body mass of the five members of *Dendrocopos* living in the Palaearctic (69.8 g ± 29.1) is 42 % larger than that of the nine members of *Picoides* living in the Nearctic (49.2 g ± 16.1; Table 1), the difference is not

Table 1. Data for Dendrocopos *in the Western Palaearctic and* Picoides *in the Nearctic. Differences between genera are denoted by * in a t-test (two-tailed).*

Variable	*Dendrocopos*				*Picoides*			
	Min-max	**Mean**	**SD**	**n**	**Min-max**	**Mean**	**SD**	**n**
Length (mm)	15-25	21.2	3.8	5	16-34	21.8	5.3	9
Body mass (g)	23-100	69.8	29.1	5	27-74	49.2	16.1	9
Egg volume index	4.3-12.4	9.5	3.1	5*	4.5-7.7	6.6	1.3	7
Egg weight	2.0-6.0	4.5	1.6	5	2.1-4.8	3.4	1.1	5
Relative egg weight	0.06-0.09	0.069	0.013	5	0.06-0.09	0.074	0.010	5
Relative egg volume	0.12-0.19	0.14	0.03	5	0.10-0.17	0.15	0.03	7
Clutch size	4.0-6.0	5.1	1.0	5*	3.2-4.6	4.1	0.4	9
Clutch size/female w.	0.04-0.26	0.10	0.09	5	0.04-0.17	0.09	0.04	9
Clutch weight	12.0-29.4	22.0	6.3	5*	9.7-16.7	13.6	2.7	5
Clutch w./female w.	0.2-0.5	0.35	0.1	5	0.2-0.4	0.31	0.1	5
Incubation period	10-12	10.9	0.7	5*	11-14	12.4	1.3	6
Incubat./female w.	0.11-0.48	0.21	0.16	5	0.17-0.44	0.28	0.10	6
Nestling period	20-27	22.8	2.7	5	15-29	23.7	4.6	7
Incubat./Nestling	1.8-2.6	2.1	0.3	5	1.1-2.5	1.9	0.5	6
Incub.+Nestl. periods	31-37.5	33.7	2.6	5	29-40.5	36.1	4.4	6
Bill dimorphism	1.01-1.08	1.05	0.03	5*	1.04-1.16	1.11	0.05	6

significant (t_{12}=1.73, p=0.11). However, the *Dendrocopos* members seem to have larger eggs (egg volume index 9.5 ± 3.19, larger clutch size (5.1 ± 1.0) and larger clutch weight (22.0 g ± 6.3) compared to the *Picoides* members (egg volume index 6.6 ± 1.3, t_{10}=2.28, p=0.046; clutch size 4.1 ± 0.4, t_{12}=2.67, p=0.020; clutch weight 13.6 g ± 2.7, t_8=2.75, p=0.025). On the other hand, the mean incubation period is markedly shorter in the *Dendrocopos* members (10.9 d ± 0.7) than in the *Picoides* members (12.4 d ± 1.3, t_9=-2.33, p=0.045).

The mean sexual dimorphism in bill length differs significantly between the genera, the *Dendrocopos* members (1.05 ± 0.03) being less dimorph than the *Picoides* members (1.11 ± 0.05, t_9=-3.22, p=0.010; Table 1).

Correlations of body mass

With one exception, all correlations between female body mass and reproductive patterns are, whether significant or not, positive or negative for both *Picoides* in the Nearctic and *Dendrocopos* in the Palaearctic (Table 2). Egg size (volume index and weight) and clutch weight increase with female body mass in both taxa, whereas clutch size tends to decrease with body mass, significantly so in *Picoides*. The total nesting time tends to increase with the female body mass in the *Dendrocopos*, significantly so in the *Picoides*. The relative egg size, relative clutch weight, and clutch size are inversely correlated with the body mass in both taxa, indicating that larger species lay relatively small eggs and have a small relative clutch size.

However, the genera *Dendrocopos* and *Picoides* provide opposite sexual dimorphism in the bill length to body mass relationship, this being positive in *Dendrocopos* (R^2=0.912, p=0.011) and negative in *Picoides* (R^2=0.306, p=0.255; Fig. 1). The rate at which dimorphism changes with body mass differs significantly among the genera (F_1=9.09, p=0.017 in a general linear model, GLM, based on the sum of square statistics).

Furthermore, the relationship between sexual bill dimorphism and body mass in the Palaearctic Three-toed Woodpecker *P. tridactylus* (dimorphism = 1.09, body mass = 60 g) indicates a closer connection to *Picoides* (*sensu* Short) than to *Dendrocopos*. Thus, if *P. tridactylus* data are included in the *Picoides* data from the Nearctic region, the dimorphism to body mass relationship increases to R^2=0.335, p=0.173, but decreases when included in the *Dendrocopos* data from the Palaearctic region (R^2=0.477, p=0.129).

Table 2. Spearman rank correlations of female body mass and reproductive patterns together with sexual bill dimorphism. Figures in bold denote significant correlation values.

Factor	*Dendrocopos*			*Picoides*		
	r_s	p	n	r_s	p	n
Egg volume index	**0.98**	0.005	5	**0.89**	0.007	7
Egg weight	**0.90**	0.037	5	**1.00**		5
Clutch size	-0.47	0.420	5	**-0.80**	0.010	9
Clutch weight	**0.90**	0.037	5	**0.90**	0.037	5
Incubation period	-0.46	0.434	5	-0.15	0.781	6
Nestling period	0.67	0.219	5	0.56	0.192	7
Total nesting period	0.60	0.285	5	**0.89**	0.037	5
Incub./nestl. period	0.70	0.188	5	0.71	0.111	6
Relative egg volume	-0.60	0.285	5	-0.68	0.094	7
Relative egg weight	-0.70	0.188	5	-0.80	0.104	5
Clutch w./body mass	-0.70	0.188	5	**-0.90**	0.037	5
Bill dimorphism	**0.98**	0.005	5	-0.67	0.148	6

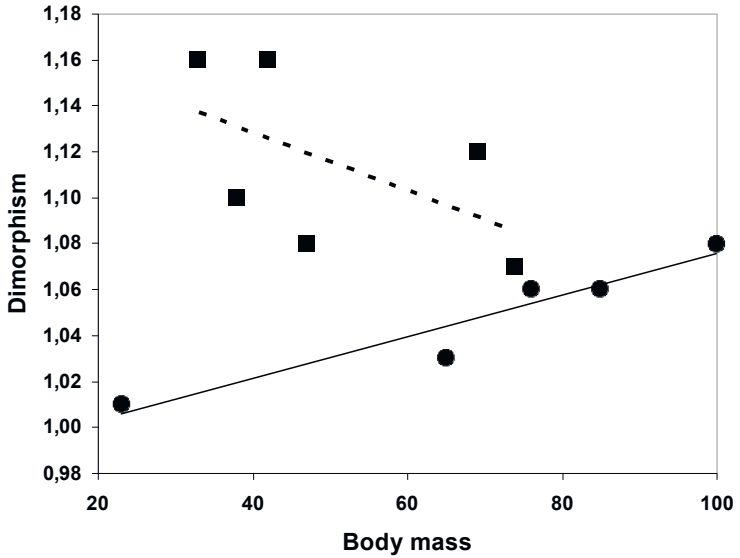

Figure 1. The relationship between female body mass (g) and sexual dimorphism (ratio of mean male to female bill length) in the genera Dendrocopos *of the Western Palaearctic and* Picoides *(*sensu *Short) in the Nearctic region.* Dendrocopos *(solid line):* $F_{1,3}=31.09$, $p=0.011$, $b_1=0.001$; Picoides *(stippled line):* $F_{1,4}=1.76$, $p=0.255$, $b_1=-0.002$.

As a consequence of the opposite sexual dimorphism to body mass relationship, *Dendrocopos* and *Picoides* also show opposite trends in the relationship between dimorphism and egg weight (*Dendrocopos*: $r_s=0.98$, $p=0.005$, $n=5$; *Picoides*: $r_s=-0.80$, $p=0.10$, $n=5$).

To summarize, the *Dendrocopos* woodpeckers tend to have larger eggs, larger clutch size and clutch weight but shorter incubation period than *Picoides* woodpeckers. However, none of these patterns are significant when the female body mass is taken into consideration. *Dendrocopos* and *Picoides* provide opposite sexual dimorphism in the bill length to body mass relationship, this being positively correlated in *Dendrocopos* and negatively correlated in *Picoides*.

DISCUSSION

Picoides (*sensu* Short) is the largest genus of woodpeckers. However, molecular data have revealed that many of the morphological and behavioural characters used to lump species into *Picoides* have evolved by convergent evolution, and it has been suggested that the genus is a conglomerate of several smaller groups (Weibel & Moore 2002a). Although the classification scheme drawn up by Short (1982) is still in use, it certainly has numerous errors at the generic level. The results of several molecular phylogenetic studies (Weibel & Moore 2002a, b, Webb & Moore 2005) strongly suggest that several remarkable cases of plumage convergence have occurred. One representative example of apparent plumage convergence is the sympatric Downy Woodpecker *Picoides pubescens* and Hairy Woodpecker *P. villosus*, which look very similar but are distantly related species (Weibel & Moore 2002a, b). Thus, plumage characters apparently are considered highly labile and of little use for determining intergeneric relationships among woodpeckers (Weibel & Moore 2005).

No clear link has been established between the relationships of Old World and New World species other than to infer that the most primitive species is Eurasian (Weibel & Moore

2002a). However, in contrast to the recent molecular systematics by Webb & Moore (2005) and Benz *et al*. (2005), Fuchs *et al*. (2007) considered the genera *Dendrocopos* to be paraphyletic and *Picoides* polyphyletic, the former with its ancestor distributed in the Old World and the latter in the New World.

The only significant difference found between the genera *Dendrocopos* in Europe and *Picoides* (*sensu* Short) in North America in the characters analysed here is the opposite relationship of sexual dimorphism in bill length to female body mass, where larger *Dendrocopos* are more dimorph and *Picoides* less so. The apparent closer connection of the Eurasiatic *P. tridactylus* to the North American *Picoides* found in the present article strengthens the supposed separation of the two genera.

Because bill length is adaptive and probably a result of competition or other types of interaction between species (Bock 1964), it may be a poor taxonomic criterion at the generic level. The opposite dimorphism to body mass relationships found between *Dendrocopos* and *Picoides* species may therefore have little taxonomic relevance, but simply be an adaptation to intra- and interspecific competition or different ecological environments (cf. Selander 1966, Hogstad 1993). As an example, woodpeckers that are dependent on wood-boring beetles, as larvae or imagines, tend to be more sexually dimorph in bill length (Hogstad unpublished data) and also have smaller clutches than those living on more varied food (Koenig 1987).

Although the classification scheme drawn up by Short (1982) is still in use, it certainly has numerous errors at the generic level. Based on phylogenetic studies with molecular character sets, Weibel & Moore (2005) retain *Dendrocopos* in *Picoides* whereas Fuchs *et al*. (2007) maintain the two genera. The opposite sexual dimorphism of the two genera, as demonstrated in the present paper, agrees with Fuchs *et al*. (2007). As most phylogenetic studies of woodpeckers are based on birds from the New World, the taxonomic classification of woodpeckers living in other geographical regions is still poorly understood and is in need of more focused studies.

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SAMMENDRAG

Forskjell i relasjonen seksuell dimorfi i nebb - vekt av hunn støtter atskillelse av slektene *Dendrocopos* og *Picoides* i klassifiseringen av hakkespetter

Klassifiseringen av slekter innenfor ordenen hakkespetter har resultert i forskjellig inndeling alt etter om den har vært basert på anatomi eller drakttegninger og geografisk utbredelse. Fylogenetiske undersøkelser de senere årene, basert på molekulære studier, har gitt vesentlige endringer. Til tross for påviselige feil, benyttes fortsatt Lester Short's taksonomiske system fra 1982. Short samlet artene innenfor slektene *Dendrocopos* og *Picoides* til *Picoides*. Dette blir fortsatt stort sett fulgt av amerikanske forskere, mens flere europeiske forskere holder de to slektene atskilt. Basert på molekulære data av hovedsakelig amerikanske fugler, føres de fleste *Dendrocopos*-arter inn under *Picoides* (Weibel & Moore 2005), mens Fuchs m.fl. (2007) opprettholder de to slektene.

På grunnlag av data fra litteraturen, blir det i denne artikkelen vist at *Dendrocopos*-artene i gjennomsnitt tenderer til å ha større egg, større kull og kullvekt, og kortere rugetid enn *Picoides*-artene, men kontrollert mot hunnens vekt er ikke forskjellen statistisk signifikant (tabellene 1 og 2). Seksuell dimorfisme i nebblengde (nebblengde hos hann/hunn i forhold til hunnens vekt) er imidlertid motsatt hos de to slektene: positiv hos *Dendrocopos*-artene i Europa og negativ hos *Picoides*-artene (*sensu* Short) i Nord-Amerika (Figur 1), noe som styrker atskillelsen av slektene.

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