

# A review of adult survival rates in woodpeckers

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Although many forestry management strategies rely on population estimates of indicator species such as woodpeckers (family Picidae), empirical estimates of demographic parameters within this taxon are few. In this review, I searched the literature for survival estimates of woodpeckers and found information for 54% of North American species and 30% of European species. The average survival rate for all woodpecker species combined was 0.58 but varied from 0.30 to 0.93 in apparently stable populations. Data were few, but there was not a consistent pattern of sex-biased mortality. Among North American species, there was a negative correlation between clutch size and survival consistent with life history theory.

## Introduction

Each species has a characteristic pattern of age-related survival and reproduction known as its life history (Stearns 1976) and most theory about the evolution of life histories assumes mortality is the driving force behind variation reproductive parameters (e.g., Cole 1954, Charlesworth 1980, Curio 1989). In confirmation of this idea, a review of avian life histories suggested that fecundity was more strongly associated with survival than it was with food supply (Martin 1995). Quantifying survival rates may therefore be important for understanding the ecological and evolutionary forces that shape an individual's behaviour. In addition, knowledge of vital rates such as survival has practical use for the conservation and management of target species (Doherty & Grubb 2002, Dinsmore *et al.* 2003). Since modern forest management is concerned with the population size of keystone species such as woodpeckers (Martin & Eadie 1999), understanding the population dynamics of this taxon

has practical applications as well as theoretical interest (McClelland & McClelland 1999).

There are several ways to estimate survival, each with advantages and disadvantages. Traditional mark-recapture techniques (the resighting rates of banded individuals) are relatively simple to compute and have been used for decades. Such resighting rates may be calculated by a variety of formulas each with slightly different assumptions (Farner 1945, Roberts 1971, Forde & Sloan 1984). Recent advances in computing software, such as program MARK (White & Burnham 1999) allow more complex modelling techniques such as the Cormack-Jolly-Seber (CJS) estimate. Advantages of these more complex models are that they allow an estimation of recapture probability (resighting efficiency), and can model biologically significant covariates while providing error estimates for model parameters (Lebreton *et al.* 1992). However, all capture-recapture models share a common limitation, the inability to separate permanent emigration from true mortality (e.g. Cilimburg *et al.* 2002). A third way

to estimate survival, through the monitoring of radio-tagged individuals, can give true survival estimates providing that the fate of all radioed individuals is known (Elchuk & Wiebe 2002). However, survival estimates may be biased when individuals are only tracked for part of the annual cycle, as is often the case with the short battery life in smaller radio transmitters.

Estimates of survival for woodpeckers have lagged behind those of other avian groups perhaps because these birds are relatively difficult to capture in large numbers (Bull 2001). A review of European woodpeckers by Pasinelli (2006) highlighted knowledge gaps about demographic parameters for nearly every species. The review of avian survival rates by Martin (1995) uncovered estimates for only seven Picid species. In this paper, my goal was to summarize current data on survival rates in Picidae, to emphasize the existing gaps in knowledge, and to test whether survival was negatively correlated with clutch size, a measure of fecundity, as predicted by life history theory.

## Material and methods

I searched the literature for information on survival rates of adult North American and European woodpeckers, relying heavily on the *Birds of the Western Palearctic* (Cramp *et al.* 1993) and on species accounts in the *Birds of North America*. I also searched electronic journal databases with the keywords “survival”, “mortality” and “woodpecker”. For North American species, I also included data from the continent-wide constant-effort mistnetting program (MAPS; Institute of Bird Populations 2003) which uses CJS models and posts peer-reviewed survival estimates on its website ([www.birdpop.org](http://www.birdpop.org)). These searches likely cover the majority of published information for each species.

Correlations were performed with SPSS (1998). Although more complex statistical methods such as phylogenetic independent contrasts are often useful for interspecific comparisons, the species in this paper come from a narrow phylogenetic subset and some previous research indicated that the same results are obtained from correlative vs. phylogenetic approaches for this subset of spe-

cies (Martin 1993). Furthermore, the phylogeny of woodpeckers is incompletely resolved, and the sample sizes here are small so the validity and the power of conclusions from the more complex models may be questionable. Because life history traits may be under different selective pressures in Europe as compared with those in North America (Martin & Clobert 1996), I analyzed North American species separately. It is wise to be cautious about comparing survival estimates in Table 1 because methodologies and sample sizes among studies differ (Karr *et al.* 1990); however, even coarse data may be sufficient to highlight general differences in life histories among species.

## Results

Survival estimates were obtained for 12 of 23 (52%) North American species and for 3 of 10 (30%) European species (Table 1). Most studies reported estimates based on the proportion(s) of colour-banded adults that returned to breed in the study area the following years. Aside from the MAPS program, the only studies to use CJS modelling of survival rates were those on northern flickers *Colaptes auratus* (Fisher & Wiebe 2006), downy woodpeckers, *Picoides pubescens* (Karr *et al.* 1990, Doherty & Grubb 2002) and red-bellied woodpeckers *Melanerpes carolinus*. Survival estimates ranged from a low of 0.29 for a population of downy woodpeckers to a high of about 0.91 for a population of red-cockaded woodpeckers *Picoides borealis* (Table 1). Excluding the former study that was based on a declining population, the average survival rate was 0.56 for North American woodpeckers, 0.63 for European woodpeckers, and 0.58 for all species combined.

Consistent with life history theory, there was a negative relationship between survival and fecundity (clutch size) among North American woodpeckers ( $r = -0.59$ ,  $n = 12$ ,  $P = 0.023$ ). However, the correlation was not quite significant with all woodpeckers pooled ( $r = -0.38$ ,  $n = 15$ ,  $P = 0.15$ ).

## Discussion

The average survival rate of 0.58 for all species of woodpeckers in this study, slightly smaller

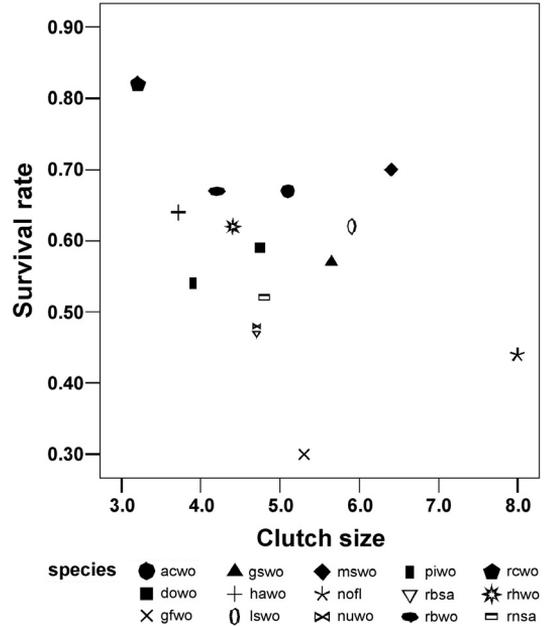
**Table 1.** Annual adult survival rates for woodpeckers (family Picidae). Recapture efficiencies are shown for Cormack-Jolly-Seber models. The four letter codes refer to the species names in the figure. Name codes with asterisks = European species.

Species	Code	Sex	Survival	<i>n</i>	Method	Source
Northern flicker <i>Colaptes auratus</i>	nofl	MF	0.47	77	CJS	MAPS
		M	0.42	239	CJS	Fisher & Wiebe 2006
		F	0.44	249	"	— " —
Red-naped sapsucker <i>Sphyrapicus nuchalis</i>	rnsa	MF	0.43	642	CJS	MAPS
		MF	0.59	29	resight	Trombino 1998
		MF	0.43	131	resight	Fleury 2000
		MF	0.65	52	resight	Walters <i>et al.</i> 2002
Red-breasted sapsucker <i>Sphyrapicus ruber</i>	rbsa	MF	0.41	590	CJS	MAPS
		MF	0.53	51	resight	Trombino 1998
Acorn woodpecker <i>Melanerpes formicivorus</i>	acwo	M	0.83	273	resight	Koenig & Stacey (1990)
		F	0.73	302		
		M	0.61	155	resight	— " — (different population)
		F	0.52	103		
Golden fronted woodpecker <i>Melanerpes aurifrons</i>	gfwo	MF	0.30	92	CJS	MAPS
Red-bellied woodpecker <i>Melanerpes carolinus</i>	rbwo	MF	0.66	103	CJS	Karr <i>et al.</i> (1990)
		MF	0.68		resight	Ingold in Martin (1995)
Red-headed woodpecker <i>Melanerpes erythrocephalus</i>	rhwo	MF	0.62		resight	Ingold in Martin (1995)
Red-cockaded woodpecker <i>Picoides borealis</i>	rcwo	M	0.90	48	resight	DeLotelle & Epting (1992)
		F	0.93	48		
		M	0.76	646	resight	Walters <i>et al.</i> (1988)
		F	0.69	717		
Downy woodpecker <i>Picoides pubescens</i>	dowo	MF	0.26	404	CJS	Doherty & Grubb (2002)
		MF	0.47	1458	CJS	MAPS
		MF	0.64	54	CJS	Karr <i>et al.</i> (1990)
		MF	0.65	138	resight	Forde & Sloan (1984)
Hairy woodpecker <i>Picoides villosus</i>	hawo	MF	0.64	463	CJS	MAPS
Nuttall's woodpecker <i>Picoides nuttallii</i>	nuwo	MF	0.48	170	CJS	MAPS
Pileated woodpecker <i>Dryocopus pileatus</i>	piwo	MF	0.43		resight	Bull & Jackson (1995)
		MF	0.47	31	radio tag	Bull (2001)
		MF	0.56	32	radio tag	Bonar (2001)
		MF	0.69	28	resight	Bull & Meslow (1988)
Lesser spotted woodpecker <i>Dendrocopos minor</i>	lswo*	M	0.67	77	resight	Wiktander <i>et al.</i> (2001)
		F	0.57	76		
Middle spotted woodpecker <i>Dendrocopos medius</i>	mswo*	MF	0.67		resight	Michalek & Winkler (2001)
		MF	0.72		other	Kossenko & Kaygorodova (2003)
Great spotted woodpecker <i>Dendrocopos major</i>	gswo*	MF	0.57		resight	Michalek & Winkler (2001)

than the 0.66 for woodpeckers in Martin (1995), is fairly similar to the 0.55 average for open-nesting passerine birds and higher than the 0.45 average reported for non-excavating passerine cavity nesters (Martin 1995). In general, mortality rates within *Picidae* appear to fall within the 0.40–0.60 range reported for small temperate-zone land-birds in other studies (Cody 1971, Ricklefs 1973, Skutch 1985). Reasons for the very low survival of golden fronted woodpeckers *Melanerpes aurifrons* are unclear and more data are needed to determine whether this is only an artifact of small sample size, or whether that population may be declining.

Assuming stable populations, life history theory suggests that species that invest heavily in current reproduction have shorter lifespans than those that invest less per breeding attempt (Reznick *et al.* 2002). This pattern seemed to be confirmed, at least among North American woodpeckers, where there was a negative correlation between survival and clutch size. At one extreme, red-cockaded woodpeckers had the highest survival rates and also the smallest clutches (Fig. 1). At the other extreme, northern flickers had the largest clutches but survival rates that averaged about half that of red-cockaded woodpeckers. Flickers may thus show a pattern of “fast” or r-selected life history with relatively heavy investment in reproduction at early ages at the expense of longevity. There were too few data to calculate life history trade-offs for the European species but the prediction is that species with relatively large clutches such as the wryneck *Jynx torquilla* and the green woodpecker *Picus viridis* would have survival rates lower than the mean for woodpeckers.

Whether heavy investment in reproduction causes increased mortality or whether extrinsic sources of mortality on adults drive them to reproduce early in life is difficult to determine (Stearns 1976, Martin 2004). One possible extrinsic source of mortality is migration. Few picids are migratory, but those which are, flickers and sapsuckers, are among the woodpeckers with the lowest survival rates (Fig. 1). No data were available for wrynecks, but if migration is costly, adult mortality should also be high in that species and may drive the large clutches. An interspecific comparison of survival among 6 species



**Fig. 1.** Relationship between survival rate and clutch size within picidae. Survival rates for each species were averaged when there were data from more than one population and the lowest survival rate of downy woodpeckers from the declining population was excluded (see Table 1). Average clutch sizes for each species were calculated from species accounts contained in the *Birds of North America* and the *Birds of the Western Palearctic*. See Table 1 for definitions of the species codes used in the legend.

of sparrows with varying migration distances (from resident to long-migration), documented no significant survival differences between residents and migrants, nor between sparrows with varying lengths of migration (Sandercock & Jaramillo 2002). However, other studies on passerines suggest that migration is costly and represents the period of highest mortality in the annual cycle (Sillett & Holmes 2002). Clearly, the mortality costs of migration versus residency are not well understood and need further study within woodpeckers and other birds.

Among the few species where survivorship was calculated for each sex individually, there was not a consistent pattern of sex-biased survival. Male acorn woodpeckers *Melanerpes formicivorus* and male lesser spotted woodpeckers *Dendrocopos minor* had higher survival than females (Table 1). However, the survival of female red-cockaded woodpeckers was higher

than males in one population. Among northern flickers, the top model suggested equal survival for the sexes, although a second model also received support and suggested that female survival was slightly higher than males (Table 1; Fisher & Wiebe 2006). Whether differences in survival between the sexes are linked to differences in reproductive investment deserves further study.

Sample sizes in this review were small, precluding sophisticated statistical models with multiple factors and independent phylogenetic contrasts. As much as anything, this should alert biologists studying woodpeckers to the need to record and publish survival estimates for their populations. There are no data for most picid species in the northern hemisphere and data for species in the southern hemisphere seem non-existent. Aside from two intensively studied cooperatively breeding species, the red-cockaded and acorn woodpeckers (e.g. Khan & Walters 1992), possible causes of intraspecific variation in mortality such as sex, age, body condition and habitat quality have scarcely been investigated. A lack of data means there are few “benchmark” survival estimates to judge the viability of local populations and whether the habitat quality is of concern (DeSante & Rosenberg 1998). As warnings are raised about the status of woodpecker populations in modified landscapes, it will become increasingly important to monitor vital rates to determine the stage of the reproductive cycle at which population change is being effected (DeSante 1992) and to most efficiently target conservation measures.

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