

Are forest and grassland grouse on different life history tracks?

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Life history theory predicts an inverse relationship between fecundity and survivorship, traits that cannot be maximized simultaneously, leading to a tradeoff (Partridge & Sibly 1991, Zera & Harshman 2001, Roff 2002). This well established tradeoff is the rule in birds (Ricklefs 1983). Body size and life span also tend to be correlated positively in birds (Lindstedt & Calder 1976, Sæther 1989). Moreover, such patterns tend to have a strong phylogenetic signal (Sæther 1989, Brawn et al. 1995)—birds within a particular taxonomic order or family tend to exhibit similar patterns in life history traits.

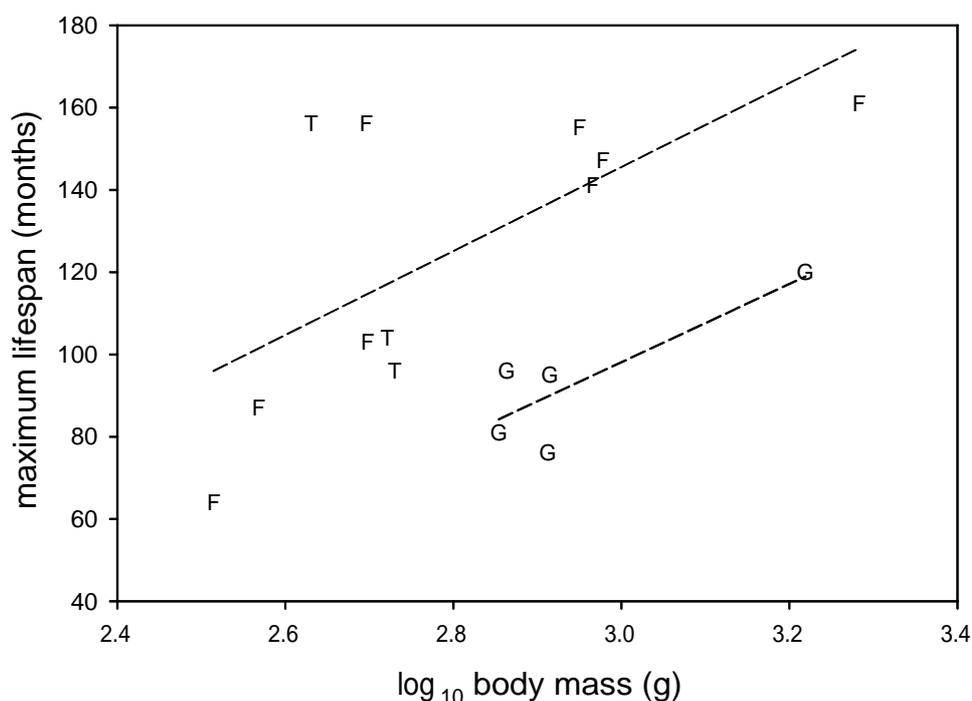


Figure 1. Maximum life span as a function of body mass for forest (F), tundra (T), and grassland (G) species of grouse. Note how tundra species—the ptarmigan (*Lagopus* spp.)—clump with the forest species whereas the grassland species have a separate but parallel relationship.

The grouse (Phasianidae: Tetraoninae) are characterized by large body size, high annual reproductive output, and, for their size, short life span. Because the grouse comprise a distinct subfamily (or a family, depending on one's taxonomy), it might be expected that all species have the same relationship between body size and life span. Yet I discovered that this was not the case while researching background for a note on life span in the lesser prairie-chicken *Tympanuchus pallidicinctus* (Wolfe, Sakoda, and Patten in prep.) and specifically how a published claimed maximum (Clapp et al. 1982) is almost certainly erroneous. For this background research I compiled a table of published maximum life spans for most grouse species (and because of their striking morphological distinctness I treated Attwater's prairie-chicken, *Tympanuchus cupido attwateri*, and the red grouse, *Lagopus l. scoticus*, separately). When plotted against body size an interesting pattern emerged (Figure 1): maximum life span was related positively to mean body size, but only if grouse of forest or tundra habitats ($r^2 = 0.45$) were treated separately from grouse of temperate grassland habitats ($r^2 = 0.71$). For each group, slopes of regression lines were similar, but intercepts differed markedly (forest/tundra: $y = 102.1x - 160.9$; grassland: $y = 95.1x - 187.1$). But why?

Such a difference in intercepts suggests that species in each group of species have distinct evolutionary histories. It is possible that the forest and tundra grouse and the grassland grouse differ in their evolutionary history. *Centrocercus* (the sage-grouse) and *Tympanuchus* (the prairie-chickens)—the grassland grouse—form a clade with *Dendragapus* (the blue grouse complex), a forest grouse, yet separate from other species of forest and tundra grouse (Drovetski 2002), meaning that they share a



phylogenetic history. Yet this common phylogenetic history is perhaps an unsatisfying explanation inasmuch as the blue grouse complex shares a life history pattern with its fellow forest grouse, not with the grassland grouse with which it shares a clade. Accordingly, even though prior research has suggested a role for habitat in grouse life history (e.g., Jönsson et al. 1990), we may need to look elsewhere for a fuller explanation of the prevailing pattern.

Looking beyond habitat preference, then, it is possible that an explanation lies more in differences in breeding system. Grouse species can be grouped into three types of breeding system or “social structure” (Wiley 1974, Wittenberger 1978): promiscuous species that lek, promiscuous species with dispersed males, and species that form pair bonds. Re-plotting body mass against maximum life span with new labels for these three groups yields a comparable pattern with parallel slopes for lekking species (Figure 2 $y = 143.0x - 318.5$, $r^2 = 0.58$) versus dispersed or paired species ($y = 137.3x - 255.4$, $r^2 = 0.37$), but, as before, intercepts differ markedly. We again see separate life history tracks, but this time the difference is driven by breeding system. Moreover, in either case the expected pattern—derived from life history theory—of a positive relationship between body size and life span would appear weaker ($y = 69.3x - 66.9$, $r^2 = 0.17$) had we lumped all grouse species together irrespective of habitat or breeding system, as has been done in prior studies (e.g., Zammuto 1986).

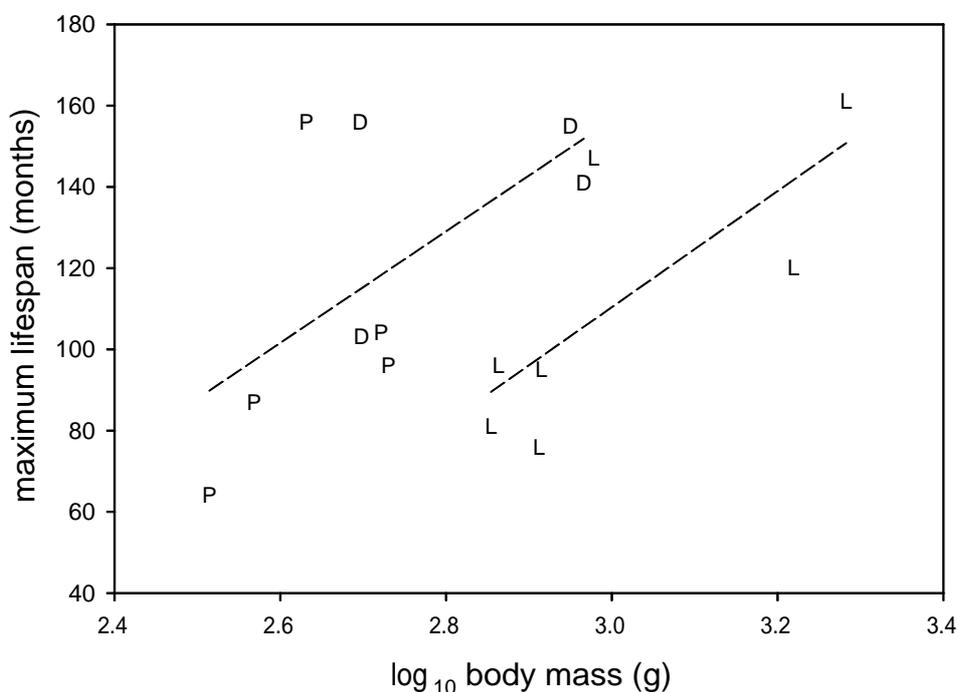


Figure 2. Maximum life span as a function of body mass for grouse species that form leks (L), have dispersed males during courtship (D), and form pair bonds (P). The resultant split pattern resembles that in Figure 1, but in this case the division is between lekking species and dispersed/paired species.

If the evolution of lekking caused a shift to a parallel track in the relationship between body size and life span, what about shifts in other life history traits related to body size? Another key prediction from theory is that clutch size should decrease with increased body size. Prior work has reported such a pattern across North American gamebirds (Zammuto 1986), including grouse, and across galliforms in general (Kolm et al. 2007). For the Tetraoninae alone, plotting clutch size against body mass yields an exceedingly weak negative relationship ($y = -1.2x + 11.6$, $r^2 = 0.02$), yet separating the subfamily by breeding system better yields the stronger negative relationships predicted by theory (Figure 3; dispersed/paired: $y = -2.1x + 13.4$, $r^2 = 0.03$; lekking: $y = -7.8x + 32.3$, $r^2 = 0.45$), although in this case slopes are not parallel and only lekking species exhibit a convincingly strong pattern. The weak relationship in dispersed/paired species is to a considerable extent driven by two species, the Chinese grouse (*Bonasa sewerzowi*) and the white-tailed ptarmigan (*Lagopus leucurus*), both of which have smaller clutch sizes than expected for their size.



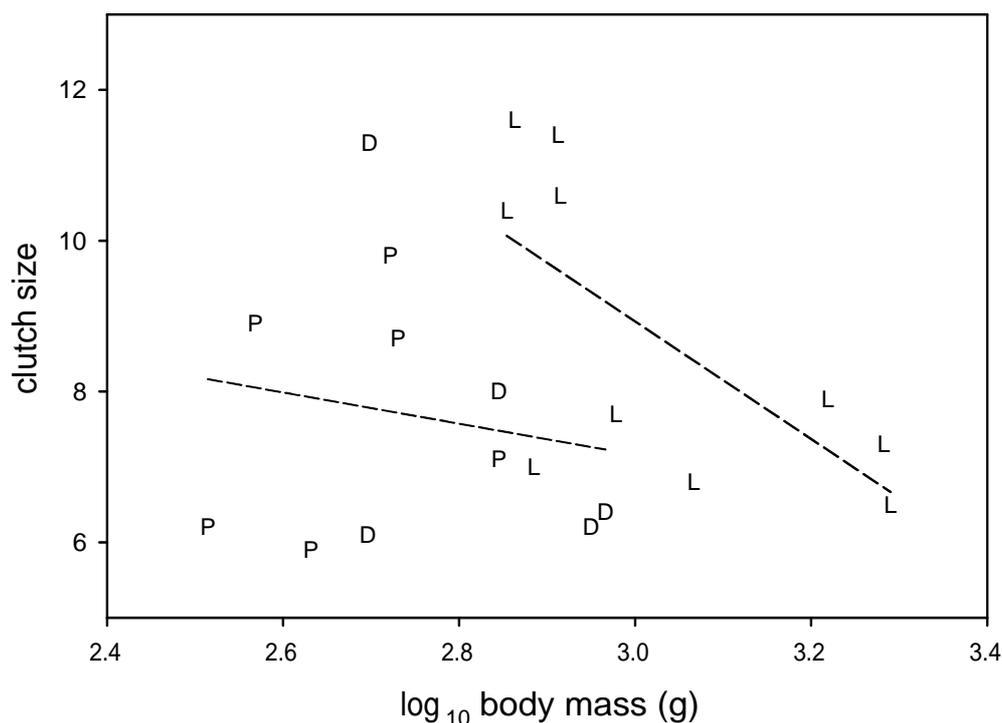


Figure 3. Mean clutch size as a function of body mass for grouse species that form leks (L), have dispersed males during courtship (D), and form pair bonds (P). In this case lekking species exhibit the strong negative association predicted by life history theory, but species with the other breeding systems exhibit only a weak association.

Life history theory predicts tradeoffs between clutch size and the extent to which males help rear young, in that “Females could be expected to adjust clutch size or other life history traits (e.g. seasonal timing of reproduction) in relation to the level of anticipated male parental care” (Svensson & Sheldon 1998). In the Tetraoninae, however, this pattern does not hold. Males of species that disperse during courtship provide no parental care, so in this respect they do not differ from males of species that lek. If we separate grouse by extent of male parental care (Wiley 1974, Wittenberger 1978), we continue to see a strong negative relationship for species with no care (Figure 4; $y = -4.3x + 21.2$, $r^2 = 0.15$) but the relationship for species that pair bond, and in which males provide at least some care, is positive (Figure 4; $y = 3.4x - 1.2$, $r^2 = 0.07$)! Evidently, the degree to which males assist in nest defense or chick-rearing does not provide a good explanation of clutch size variation relative to body mass, at least in light of life history theory.



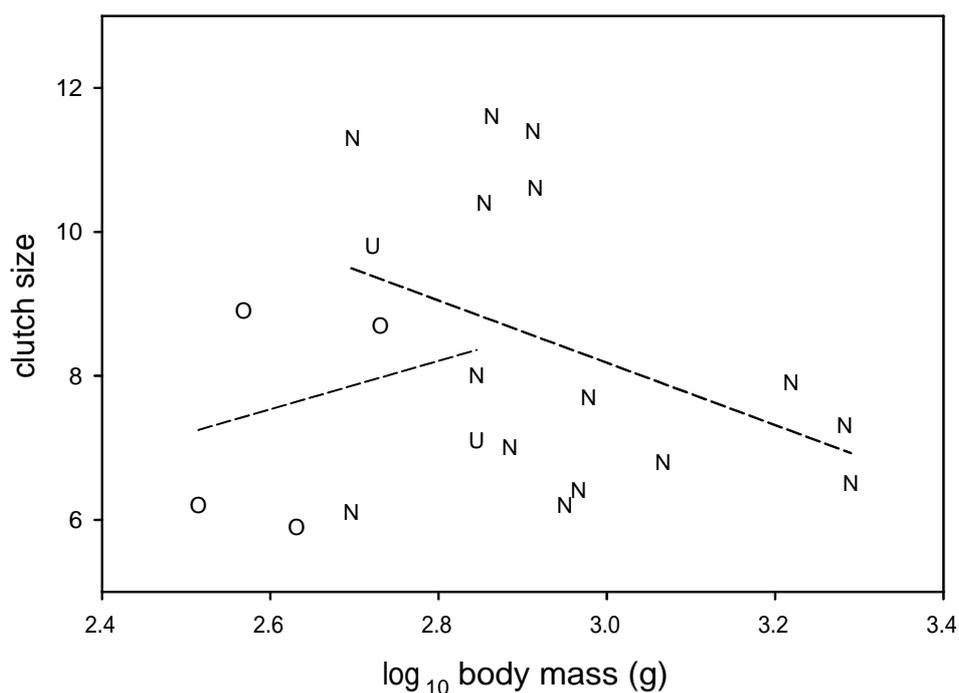


Figure 4. Mean clutch size as a function of body mass for grouse species in which males never provide parental care (N) versus species that occasionally (O) or usually (U) provide at least some care, including nest guarding.

I conclude that although it appears that species of grassland grouse are on a different life history track from species of forest and tundra grouse, the underlying cause is not one of habitat differentiation. Rather, evolution of lekking in some grouse has led to divergent life histories. Expected relationships hold for both life span and clutch size, but these relationships are on roughly parallel tracks associated with breeding system. Expected relationships are not evident, by contrast, relative to the extent of male parental care. Clearly, more work is needed in teasing apart life history divergence within the Tetraoninae. Life history theory, both in terms of predicted tradeoffs and directions of associations, has been supported by various empirical studies in the grouse (e.g., Wiley 1974, Zammuto 1986, Jönsson et al. 1991, Patten et al. 2005, Kolm et al. 2007). It remains to be determined, however, if patterns hold throughout the subfamily or if evolution has produced divisions within the subfamily.

References

- Brawn, J.D., Karr, J.R. & Nichols, J.D. 1995. Demography of birds in a Neotropical forest: Effects of allometry, taxonomy, and ecology. – *Ecology* 76: 41–51.
- Clapp, R.B., Klimkiewicz, M.K. & Kennard, J.H. 1982. Longevity records of North American birds: Gaviidae through Alcidae. – *Journal of Field Ornithology* 53: 81–124.
- Drovetski, S.V. 2002. Molecular phylogeny of grouse: Individual and combined performance of W-linked, autosomal, and mitochondrial loci. – *Systematic Biology* 51: 930–945.
- Jönsson, K. I., Angelstam, P. K. & Swenson, J. E. 1991. Patterns of life-history and habitat in Palaearctic and Nearctic forest grouse. – *Ornis Scandinavica* 22: 275–281.
- Kolm, N., Stein, R.W., Mooers, A.Ø., Verspoor, J.J. & Cunningham, E.J.A. 2007. Can sexual selection drive female life histories? A comparative study on Galliform birds. – *Journal of Evolutionary Biology* 20: 627–638.
- Lindstedt, S.L. & Calder, W.A. 1976. Body size and longevity in birds. – *Condor* 78: 91–94.
- Lucchini, V., Höglund, J., Klaus, S., Swenson, J. & Randi, E. 2001. Historical biogeography and a mitochondrial DNA phylogeny of grouse and ptarmigan. – *Molecular Phylogenetics and Evolution* 20: 149–162.
- Partridge, L. & Sibly, R. 1991. Constraints in the evolution of life histories. – *Philosophical Transactions of the Royal Society of London, Series B* 332: 3–13.



- Patten, M.A., Wolfe, D.H., Shochat, E. & Sherrod, S.K. 2005 Habitat fragmentation, rapid evolution and population persistence. – *Evolutionary Ecology Research* 7: 235–249.
- Ricklefs, R.E. 1983. Comparative avian demography. – *Current Ornithology* 1: 1–32.
- Roff, D.A. 2002. Life history evolution. – Sinaur Associates, Sunderland, Massachusetts, 2nd edition.
- Sæther, B.-E. 1989. Survival rates in relation to body weight in European birds – *Ornis Scandinavica* 20: 13–21.
- Svensson, E. & Sheldon, B.C. 1998. The social context of life history evolution. – *Oikos* 83: 466–477.
- Wiley, R.H. 1974. Evolution of social organization and life-history patterns among grouse. – *Quarterly Review of Biology* 49: 201–227.
- Wittenberger, J.F. 1978. The evolution of mating systems in grouse. – *Condor* 80: 126–137.
- Zammuto, R.M. 1986. Life histories of birds: Clutch size, longevity, and body mass among North American game birds. – *Canadian Journal of Zoology* 64: 2739–2749.
- Zera, A.J. & Harshman, J.G. 2001. The physiology of life history trade-offs in animals. – *Annual Review of Ecology and Systematics* 32: 95–106.

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