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Review article

Trends in grouse research

Robert Moss, Ilse Storch & Martin Müller

Biological research on birds of the grouse family has become increasingly related to conservation. We review trends in grouse biology, analysing the representation of species and topics in the titles of 2,788 papers published since 1930. Ruffed grouse *Bonasa umbellus*, the most frequently studied species before 1960, was overtaken by willow ptarmigan *Lagopus lagopus* in the 1970s, after which black grouse *Tetrao tetrix* and capercaillie *Tetrao urogallus* became increasingly popular until they were the most-studied species in the 2000s. The new focus on conservation ecology involves increased interest in the topics of threatened taxa, genetics and conservation. A new appreciation of the role of large, landscape-scale processes in population dynamics and conservation management is shown by an increase in publications on landscape ecology and habitat, enabled by technical advances in telemetry, genetics and mapping systems. Meanwhile, the number of papers on disease, diet, behaviour and reproduction has declined. The topics of climate change, human disturbance and pollution had few hits, but we anticipate that interest in them will increase as the current emphasis on conservation continues. This may well involve improved genetic and GIS techniques for determining dispersal patterns, habitat connectivity and population viability, along with a better understanding of how grouse survive their predators and other enemies. Better communication of experiences in management for grouse conservation is needed.

Key words: grouse, grouse conservation, research trends, Tetraonidae

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Field biologists studying warm-blooded animals tend to identify with their research species, and with others working on the same species. Thus 'grouse biology' is not a scientific discipline, but rather the natural communication system of people who study birds of the grouse family Tetraonidae. Although grouse biologists have no dedicated journal equivalent to for example the Journal of Raptor Research, they can meet triennially at the International Grouse Symposia. This review began with the remark by Larry Ellison, Editor of the 10th International Grouse Symposium held in 2005 (Ellison 2007), that the Symposium had more presentations concerning habitat than population biology. Also, whilst reflecting on the 8th International Grouse Symposium held in 1999, Storch (2000) concluded that towards the end of the 20th century, population dynamics, habitat and behaviour were the most frequently studied topics in grouse research. Emerging trends were population genetics and landscape ecology. These topics were both enabled by technological advances and demanded by increasing conservation needs. We revisit and update the subject of trends in grouse research and discuss possible future directions.

Although grouse research is a small part of wildlife biology, it inevitably reflects broad trends in biological science as a whole. Funding is an important determinant of such trends. In the UK, for example, scientific funding during much of the 20th century was informed by Haldane (1918), which was taken to mean that scientists and not politicians should decide how research funds are spent. This all changed following Rothschild (1971): "However distinguished, intelligent and practical scientists may be, they cannot be so well qualified to decide what the needs of the nation are, and their priorities, as those responsible for ensuring that those needs are met", namely the government. More widely, "Universities in many EU states are experiencing pressure to move towards the British model ...which has been accompanied by the decline in academic freedom in the UK" (Karran 2007).

This exemplifies a general perception that science today should be seen to be useful for some direct application. People and politicians, as well as scientists and their funding agencies, join in recognising an increased need to protect species and ecosystems from mankind. Based on this and on the trends recognised a decade ago (Storch 2000), we might expect conservation concerns to become a major motivation of grouse research in the new millennium. If so, we would expect the biological literature to pay greatest attention to red-listed grouse species and populations, and to the causes of their declines and extinctions.

Methods

We searched the scientific literature for titles of papers using the first statement in Table 1, and categorised the returns according to species (see Table 1) and topic (Table 2). The first search statement included the general terms 'grouse' and 'Tetraoni*', and so the total number of papers exceeded the sum of hits for all named species (see Table 1) or topics (see Table 2). To check reliability, we initially compared results using two data banks: Web of Science (WOS; available at: http://apps.isiknowledge.com) and BIOSIS (available at: http://ovidsp.tx.ovid.com).

For analysis, the number of hits per species (see Tables 1 and 3) or topic (see Tables 2 and 4) was categorised according to 'decade': before 1960, 1960-1969, 1970-1979, 1980-1989, 1990-1999 and 2000-2008 (data for 2008 were for part of the year only). The continuous variable 'time' was defined by assigning a numeral (0, 1, 2, 3, 4, 5) to each decade.

The earliest papers returned by WOS were from 1945, but the papers returned by BIOSIS were from 1930. So when comparing the two data banks, we excluded papers from before 1960. This comparison used logistic regressions for each species or topic, respectively ('species/topic' for short) with (hits per species/topic)/(hits for all species/topics) as the

Table 1. Species and search statements.

Species	Search statements
Any grouse	grouse OR capercaillie OR ptarmigan OR Tympanuchus OR Tetraoni*
Black-billed capercaillie	black billed capercaillie OR tetrao parvirostris OR tetrao urogalloides
Black grouse	black grouse OR tetrao tetrix OR lyurus tetrix
Blue grouse	blue grouse OR dendragapus obscurus
Capercaillie	capercaillie OR tetrao urogallus
Caucasian black grouse	caucasian black grouse OR tetrao mlokosiewiczi OR lyurus mlokosiewiczi OR caucasian grouse
Chinese grouse	chinese grouse OR bonasa sewerzowi OR chinese hazel grouse
Greater prairie-chicken	greater prairie chicken OR tympanuchus cupido
Greater sage-grouse	greater sage grouse OR centrocercus urophasianus
Gunnison sage-grouse	gunnison sage grouse OR centrocercus minimus
Hazel grouse	hazel grouse OR bonasa bonasia OR tetrastes bonasia OR tetrao bonasia
Lesser prairie-chicken	lesser prairie chicken OR tympanuchus pallidicinctus
Rock ptarmigan	rock ptarmigan OR lagopus mutus OR lagopus muta OR tetrao alpinus
Ruffed grouse	ruffed grouse OR bonasa umbellus
Sharp-tailed grouse	sharp tailed grouse OR tympanuchus phasianellus OR pediocetes phasianellus
Siberian grouse	siberian grouse OR siberian spruce grouse OR dendragapus falcipennis OR falcipennis falcipennis OR tetrao falcipennis
Spruce grouse	spruce grouse OR dendragapus canadensis OR falcipennis canadensis OR canachites canadensis
White-tailed ptarmigan	white tailed ptarmigan OR lagopus leucura OR lagopus leucurus
Willow ptarmigan	willow ptarmigan OR willow grouse OR lagopus lagopus OR tetrao lagopus OR tetrao albus OR lagopus albus

Table 2. Topics and search statements.

Topic	Search statements
Behaviour	behavio* OR etholog* OR mating OR lek* OR arena OR social OR socio* OR (mate AND choice) OR display
Climate change	climat* change OR global warming
Conservation	conserv* OR protect* OR preserv* OR (viability AND analysis)
Diet	diet OR nutri* OR food OR feed* OR fat OR protein* OR fiber
Disease	disease* OR parasit* OR worm OR nematod* OR cestod* OR endoparasite*
Distribution	distribution OR (range NOT home)
Genetics	genetic* OR gene OR DNA OR phylogen* OR kin OR kinship OR microsat* OR (minimum AND viable AND population) OR mitochon*
Habitat	habitat* OR tundra OR boreal OR forest OR montane OR alpine
Human disturbance	disturb* AND (recreatio* OR sport OR ski* OR hunt* OR leisure OR human OR tourism)
Hunting	hunt* OR harvest* OR shoot* OR bag* OR exploit*
Landscape ecology	landscape OR fragment* OR patch* OR metapop* OR spatial OR connectiv*
Management	manag*
Morphology	morpholo* OR anatom* OR feather* OR color pattern OR molt* OR plumage
Movements	movement* OR home range* OR dispers* OR migrat*
Physiology	physiol*
Pollution	chernobyl OR radiocaesium OR acid rain OR contamin* OR toxi*
Population dynamics	(population AND dynamic*) OR cycle OR density dependen* OR time series OR recruit* OR fluctuat* OR stable OR unstable OR demograph*
Predation	predat* OR (numerical AND response)
Release	releas* OR captiv* OR restock* OR introduc* OR reintroduc* OR transloc*
Reproduction	chick OR chicks OR nest* OR breed* OR brood OR hatch* OR egg* OR reproduct*
Taxonomy	taxonom* OR systemat* OR race* OR subspecies*
Threatened taxa	threat* OR endanger* OR declin* OR extirpat* OR extinct* OR poach*
Weather	weather OR rain OR temperatur*

dependent variable and the categories 'data bank', 'decade' and their interaction as explanatory variables. A significant interaction would indicate that the two data banks showed different temporal trends.

For subsequent questions, we confined analyses to BIOSIS (see Results). The first such question was whether the sum of hits per decade for all named species (see Table 1) or all topics (see Table 2), expressed as a ratio to the total number of papers involving grouse, showed any trend over time. This was tested by Poisson regressions with the sum of hits for all named species/topics as the dependent variable, time as the continuous explanatory variable, and total grouse papers as the offset. Ratios could exceed 1:1, because there could be more than one species/topic per paper.

Temporal variation for each species and topic, respectively, was tested by logistic regressions with decadal frequency ((hits per species/topic)/(total hits for all species/topics)) as the dependent variable and decade as the categorical explanatory variable.

The frequency of several species/topics typically fluctuated together over the decades, according to the zeitgeist. To quantify such broad temporal patterns, we performed principal components analyses (PCA) with the proportion of hits within each decade, for each species/topic, as the unit of analysis. This focussed on changes within a species/topic across the decades, and took no account of differences among the number of total hits for each species/topic. Species/topics with a total of < 10 hits were excluded from PCAs.

Results

Differences between data banks

The two data banks gave similar results for topics, but not for species. Of the 18 species, there were too few hits for four (see Table 3) to draw conclusions. Otherwise, black grouse and hazel grouse *Bonasa bonasia* had a significantly greater proportion of total hits in BIOSIS than in WOS, blue grouse *Dendragapus obscurus* and spruce grouse *Dendragapus canadensis* vice versa. Also, for black grouse

Table 3. Hits (BIOSIS) by species and decade, ordered by eigenvector for first principal component (EV1(s)), indicating species of currently increasing interest. Categorical differences among decades (logistic regression): **** $P < 0.0001$, *** $P < 0.001$, ** $P < 0.01$, *$P < 0.05$, otherwise not significant (rock ptarmigan) or very few hits (-). Species with < 10 hits were not included in principal component analysis. EV1(s) accounted for 46% of the variation in the data. Grouse hits > species hits because some papers on grouse did not mention a species in their title.

	Hits, % of total for all species, by species and decade								
Species	1930-1959	1960-1969	1970-1979	1980-1989	1990-1999	2000-2008	Total hits	EV1(s)	IUCN red list
Chinese grouse***	0.0	0.0	0.0	0.0	0.9	1.5	12	0.385	Near Threatened
Capercaillie****	11.9	13.7	8.6	13.6	20.3	20.3	374	0.365	Least Concern
Black grouse****	3.2	11.3	5.9	11.3	15.0	19.2	294	0.360	Least Concern
Greater sage-grouse****	3.2	2.0	0.5	2.9	3.1	11.4	99	0.347	Near Threatened
Lesser prairie-chicken***	1.1	1.2	1.7	1.6	1.5	5.4	54	0.324	Vulnerable
Hazel grouse****	2.7	7.4	3.6	1.3	10.3	6.0	130	0.224	Least Concern
Greater prairie-chicken*	3.2	5.1	1.4	1.4	3.5	3.0	66	0.109	Vulnerable
Rock ptarmigan	2.2	4.3	6.7	7.2	5.9	5.8	142	0.065	Least Concern
White-tailed ptarmigan**	0.5	1.2	4.3	1.1	2.2	2.4	51	0.018	Least Concern
Willow ptarmigan****	4.9	13.7	25.9	28.8	15.0	11.0	447	-0.143	Least Concern
Sharp-tailed grouse**	11.4	4.3	4.5	3.6	5.7	3.0	116	-0.154	Least Concern
Ruffed grouse****	46.5	19.1	18.8	11.8	7.7	7.1	355	-0.232	Least Concern
Spruce grouse****	3.2	5.1	8.1	6.4	4.4	1.7	121	-0.293	Least Concern
Blue grouse****	5.4	10.2	9.5	8.9	3.1	0.4	145	-0.337	Least Concern
Siberian grouse	0.5	1.2	0.2	0.0	0.4	0.2	8	-	Near Threatened
Caucasian black grouse	0.0	0.4	0.0	0.0	0.4	0.9	7	-	Near Threatened
Black-billed capercaillie	0.0	0.0	0.5	0.2	0.5	0.0	6	-	Least Concern
Gunnison sage-grouse	0.0	0.0	0.0	0.0	0.2	0.6	4	-	Endangered
Species, total hits	185	256	421	559	546	464	2431		
Grouse, total hits	251	290	488	599	624	536	2788		

and capercaillie, there were significant data bank-decade interactions, which meant that temporal changes for these two species differed according to data bank. This was largely because, for each species, BIOSIS showed a greater proportion of hits in the 1960s. Even so, WOS and BIOSIS each showed an increasing trend for black grouse and capercaillie from the 1970s onwards, so the two data banks agreed in this respect. We continue, using BIOSIS only, because it covered a wider range of the literature and returned more hits.

Temporal changes

Number of classified hits per grouse paper

There was no significant trend in the number of hits for all named grouse species per paper involving grouse, which remained at about 0.88 hits per paper per decade. There was, however, a significant trend for all topics, the ratio of which increased at a rate of about 14% per decade (parameter estimate 0.140 ± 0.014 (SE)), from 0.58 for papers from before 1960 to 1.14 for those from 2000-2008. This could have been because earlier papers were more likely to be concerned with topics not in Table 2, or because earlier papers had more general titles.

Species

Species with most hits overall were willow ptarmigan (447), capercaillie (374), ruffed grouse (355) and black grouse (294), while black-billed capercaillie *Tetrao parvirostris*, Caucasian black grouse *Tetrao mlokosiewiczi*, Siberian grouse *Dendragapus falcipennis* and Gunnison sage-grouse *Centrocercus minimus* each had < 10 hits (see Table 3). The popular species showed different patterns. Thus, the proportion of hits on ruffed grouse declined six-fold from pre-1960 to post-1990, willow ptarmigan peaked in the 1960s and 1970s, while black grouse and capercaillie increased from the 1970s onwards.

PCA picked out species that showed correlated temporal changes irrespective of their contribution to the total number of hits. Thus, weightings (eigenvectors) for the first principal component (see Table 3) nicely reflect the recent zeitgeist among grouse biologists. These weightings highlight species that have been increasingly reported upon in recent years

Table 4. Hits by topic and decade, ordered by eigenvector for first principal component (EV1(t), topics of currently increasing interest). EV1(t) accounted for 46% of the variation in the data. Same notation used for significance as in Table 3.

Topic	Hits, % of total for all topics, by decade						Total hits	EV1(t)
	1930-1959	1960-1969	1970-1979	1980-1989	1990-1999	2000-2008		
Genetics***	2.8	0.0	1.4	0.9	3.7	8.5	89	0.309
Conservation****	1.4	1.6	0.0	0.4	2.6	4.3	49	0.303
Threatened taxa*	2.1	0.5	1.1	2.0	2.1	4.8	61	0.292
Predation*	4.1	2.2	1.7	2.2	5.2	4.1	85	0.278
Landscape ecology****	0.0	0.5	0.8	2.7	5.3	6.9	94	0.274
Habitat***	6.9	8.2	8.4	10.1	13.9	16.1	295	0.272
Management***	0.0	2.7	1.1	1.1	3.7	3.4	59	0.182
Distribution	6.2	4.4	3.1	2.9	3.6	5.1	97	0.149
Hunting	4.1	2.7	3.9	2.2	2.4	3.4	73	0.017
Taxonomy****	9.7	2.7	0.0	0.7	0.6	1.0	33	0.009
Disease****	15.2	6.6	3.3	2.3	3.7	3.4	103	-0.002
Reproduction****	9.7	9.3	19.2	22.2	17.6	12.8	410	-0.077
Population dynamics	6.2	4.9	5.0	7.2	3.4	4.8	126	-0.140
Physiology**	0.0	0.5	2.8	0.5	0.6	0.2	19	-0.182
Movements	3.4	7.1	5.6	6.1	3.9	5.1	127	-0.185
Release**	1.4	3.8	5.6	4.3	4.5	1.5	90	-0.210
Behaviour****	8.3	19.2	15.9	13.9	13.2	8.2	313	-0.247
Weather	1.4	3.3	2.2	3.1	1.3	1.0	47	-0.277
Morphology**	3.4	4.4	4.7	2.5	1.0	1.3	58	-0.279
Diet****	13.8	14.3	14.2	12.4	6.9	3.1	228	-0.305
Pollution	0.0	0.5	0.0	0.4	0.6	0.0	7	-
Climate change	0.0	0.0	0.0	0.0	0.0	0.7	4	-
Human disturbance	0.0	0.0	0.0	0.0	0.0	0.5	3	-
Topics, total hits	145	182	359	555	619	610	2470	

(e.g. eigenvectors > 0.3: capercaillie, black grouse, Chinese grouse *Bonasa sewerzowi*, greater sage-grouse *Centrocercus urophasianus*, lesser prairie-chicken *Tympanuchus pallidicinctus*), in contrast to species about which fewer papers have been written (eigenvector < -0.3: blue grouse; < -0.2: spruce grouse, ruffed grouse).

Before 1960, almost half the hits were for ruffed grouse, reflecting early interest in this species by pioneers of grouse biology. In the 1970s, ruffed grouse were overtaken by willow ptarmigan (including red grouse *Lagopus lagopus scoticus*), and in the 1980s, ruffed grouse were more or less equalled by capercaillie and black grouse, while willow ptarmigan remained the most frequently mentioned species. In the 1990s, capercaillie had overtaken willow ptarmigan, and in the 2000s, capercaillie and black grouse had the most hits.

The increasing rate of publications on capercaillie and black grouse was reflected in their high principal component weightings (see Table 3), whilst the declining attention paid to ruffed grouse and willow ptarmigan gave them negative weightings. Apart from capercaillie and black grouse, the other three species with weightings > 0.3 are, according to the IUCN Red List of Threatened Species (IUCN 2010), either Near Threatened (Chinese grouse, greater sage-grouse) or Vulnerable (lesser prairie-chicken). More broadly (see Table 3), the seven species with the highest weightings (> 0.1) are either regionally red-listed Old-World woodland (including forest) grouse (three species; Storch 2007) or globally Vulnerable/Near Threatened (four species; IUCN 2010). The seven species with weighting < 0.1 are all of Least Concern, and include the three ptarmigan, the three New-World woodland grouse, plus the sharp-tailed grouse *Tympanuchus phasianellus* (IUCN 2010).

Four species with few hits were not included in the zeitgeist PCA. These included the Gunnison sage-grouse, which has been recognised only recently (Young et al. 2000). This species is Endangered according to the IUCN Red List of Threatened Species (IUCN 2010), and may be of increasing interest. For the other three, the bias of the BIOSIS sample towards western literature may give a false impression. Nonetheless, of the four species with few hits, the three with small or fragmented ranges are classed by the IUCN as Near Threatened or Endangered while the black-billed capercaillie, which is widespread, is of Least Concern.

In short, the literature according to BIOSIS shows two broad recent trends concerning species. First, a high or increasing frequency of papers on the Old-World woodland grouse (especially capercaillie and black grouse) has gone along with fewer papers on the New-World woodland grouse. Second, more attention has been paid to species of conservation concern. In fact, as we shall discuss, this can be seen as a single trend, with more attention to species threatened either globally (IUCN 2010) or regionally (capercaillie and black grouse in western Europe).

Topics

Topics with most hits overall (> 200, see Table 4) were reproduction, behaviour, habitat and diet. Interest in reproduction, behaviour and diet, however, seems to have declined, whereas habitat is winning more attention. Other declining topics include morphology and release, while more has recently been written about conservation, genetics, landscape, management and threatened taxa. Climate change, human disturbance and pollution each had < 10 hits.

The first principal component (see Table 4) reflected the current zeitgeist with high weightings (eigenvectors) for topics that showed an increasing proportion of hits in the 1990s and 2000s contrasted with a lower proportion in the 1960s, 1970s and 1980s (weighting > 0.2: genetics, conservation, threatened taxa, predation, landscape and habitat). It gave low weightings (< -0.2) to release, behaviour, weather, morphology and diet.

Discussion

Storch (2000) showed that population dynamics, habitat and behaviour were the most frequently studied topics of grouse research in the 1990s, and that genetics and landscape ecology were emerging trends at the end of the 20th century. Our analysis confirms this result using a different data bank and more quantitative methods. Our general finding is that, in the new millennium, biological studies of grouse have become increasingly related to conservation and to species of conservation concern. We elaborate below.

Biases of methods

The number of hits for all named species (see Table 1), per paper involving grouse, remained at about 0.88 hits per paper throughout. For named topics (see Table 2), however, the equivalent ratio almost doubled over the period studied. Reasons include the fact that more early papers were general natural history accounts not retrieved by our topic searches, new methods of study emerged, and different scientific problems were tackled. Also, we probably omitted some topics that were once fashionable, but to which little attention is now paid.

We used BIOSIS to sample the biological literature on grouse. The comparison between BIOSIS and WOS revealed that, for species at least, different data banks showed somewhat different patterns. Thus, in the case of woodland grouse, BIOSIS returned more hits for two Old-World species (black and hazel grouse) while WOS favoured two New-World species (blue and spruce grouse). More importantly, temporal trends in data from the two data banks differed slightly for black grouse and capercaillie. No such problem was apparent for topics, but we nonetheless enter the caveat that search results may differ according to the data banks used.

Species

Reasons for studying grouse include academic interest in their population processes and hunting management including (especially in North America) the setting of bag limits. In recent decades, concern for threatened populations has come to the fore and this is reflected in high principal component weightings for threatened species (see Table 3). At first blush, the increased focus on Old-World woodland grouse seems not to fit this pattern, because all three (capercaillie, black grouse and hazel grouse) are classed by the IUCN (2010) as of Least Concern but have high weightings (see Table 3). However, capercaillie and black grouse in the south and west of their range are often of national or regional (e.g. EU) conservation concern. This generates funding opportunities for studies on grouse, and many papers on these two species are motivated by conservation. Hazel grouse are generally less popular and also less studied than capercaillie and black grouse. They may therefore not conform so well to the above generalisations, and the number of hits for hazel grouse decreased somewhat after a high in the 1990s. In general, academic interest in all three western European woodland grouse has remained high since the 1990s.

None of the American woodland grouse species is threatened at national or global levels (Storch 2007). This, along with decreasing academic interest, may explain why publications on North American woodland grouse show an opposite trend to European ones. Of prairie grouse, however, both the lesser prairie-chicken (recognised as Vulnerable in 2000) and the greater sage-grouse (recognised as Near Threatened in 2004) were recently recognised by the IUCN, and this global classification was associated with a threefold increase in hits between the 1990s and 2000s (see Table 3). No such increase in interest, however, was apparent for the greater prairie-chicken *Tympanuchus cupido*, which also became recognised as Vulnerable in 2004 (IUCN 2010). Its subspecies, Attwater's prairie-chicken *T. c. attwateri*, however, was one of the first taxa listed under the US Endangered Species Act of 1966 (Morrow et al. 2004), and received much attention throughout the 1990s, when 17 out of 30 papers on the subspecies were published. This earlier attention to the subspecies masked the increased interest in the species as a whole after its IUCN listing.

Topics

Broad trends

Just as the recent zeitgeist includes increasing interest in species or populations of conservation concern, so the topics studied have become increasingly oriented towards conservation. Five of the six topics with first principal component weightings > 0.2 comprise threatened taxa, genetics and conservation (reflecting a new focus on conservation biology), plus landscape ecology and habitat (reflecting a new appreciation of the role of large-scale processes in conservation management). Predation (weighting 0.278) is included in this group of six, possibly because workers see it as a menace to the persistence of small, threatened populations. Also, its proportion of hits was the same pre-1960 as in the 2000s, so reflecting a lessening of interest in predation in the 1970s and 1980s as much as renewed interest in the 1990s and 2000s.

Several topics with many total hits (see Table 4) now get less attention than previously. Thus, of the seven topics with > 100 total hits, only one (habitat) achieves a positive principal component weighting. Diet is a spectacular example, with a fourfold decline in hits since the 1980s, the opposite trend to habitat. Whereas disease was the most popular topic pre-1960s, it had shown a fourfold decline by the 2000s. The topic with most hits overall, reproduction, remained popular, but hits declined twofold between their peak in the 1970s and the 2000s. Interest in behaviour peaked in the 1960s, but then showed a steady decline, and it has a low first principal component weighting. Two perennially popular topics, movements and population dynamics, showed no significant variation in the frequency of hits.

In short, the recent zeitgeist apparently comprises an increased interest in species of conservation concern and conservation-oriented topics, along with a declining interest in disease, diet, behaviour and reproduction. A topic, however, is more mutable than a species. The current academic publication system makes authors phrase their titles according to the current zeitgeist, and so the title of a paper probably reflects when it was written more closely than when the study was done. In general, methods, problems and social priorities change, and therefore the connotations of a phrase or search statement may alter over time. We discuss some examples in the following.

Population dynamics

Cyclic fluctuations in animal population densities were one of the first problems in quantitative ecology (Elton 1924), and continue to fascinate ecologists (Kendall et al. 1999, Turchin 2003). Such unstable dynamics are well-known among northern vertebrates, including several species of grouse. They have usually been explained as extrinsic, trophic interactions between predators and prey or between hosts and parasites (Turchin 2003).

Nonetheless, there is now good evidence that aggressive, territorial behaviour destabilises red grouse populations (Moss et al. 1996, Mougeot et al. 2003, Matthiopoulos et al. 2005) and this is of wide ecological interest (Chapman et al. 2009).

Predictions from the idea that kin selection might cause changes in aggressiveness and so destabilise grouse population dynamics (Mountford et al. 1990) could be rigorously tested only when DNA techniques for measuring relatedness between animals had been developed (Piertney et al. 2008).

In future, we expect a better understanding of how genetic processes influence population dynamics to come with the application of game theory. Thus, explanations of how altruism evolved suggest that cooperation occurs when individuals benefit more from helping each other than from behaving selfishly (Keller 1999, Lehmann & Keller 2006). Models with individuals either cooperating or acting selfishly typically result in unstable population fluctuations (Doebeli & Hauert 2005, Burtsev & Turchin 2006). Increasing populations go along with more cooperation, declines with increased selfishness. Hence, there is a broad theoretical basis for the idea that variations in the behaviour of individuals can cause unstable population dynamics.

It has also become apparent that population dynamics can depend on the scale and structure of an animal's habitat (Segelbacher et al. 2008). Thus, metapopulation theory has developed to deal with the dynamics of fragmented populations (Opdam 2004). A separate point is that unstable dynamics seem to require large areas of contiguous habitat for their expression (Moss & Watson 2001), so that habitat fragmentation may be accompanied by loss of population cycles (Watson & Moss 2004). Also, landscape-scale travelling waves in grouse populations suggest that dispersal may play a role in synchronising fluctuations in grouse populations across large areas (Moss et al. 2000, Sherratt & Smith 2008).

In short, the search statement 'population dynamics' showed no significant change in frequency (see Table 4), but developed from an accounting of animal numbers via their vital rates, to a topic that involves birds' genotypes and behaviour on the small scale, and their dispersal and distribution of habitat on a landscape scale. This synthetic advance has depended on the development of statistical and genetic techniques and Geographical Information Systems (GIS).

Genetics and taxonomy

Papers about genetics and taxonomy each showed an early peak pre-1960 (see Table 4), when they were based largely on morphology and behaviour. Decades later, taxonomy gained new impetus from DNA evidence. This is shown in Table 4 as a recent increase in hits on 'genetics' but not 'taxonomy', which appears to be the less fashionable word. New DNA-based studies of phylogenetic relationships and evolution, for example, challenge the idea that grouse evolved in the Old World (Potapov 1985) with evidence that they did so in the New World (Drovetski 2003, Pereira & Baker 2006). Also, DNA evidence has facilitated the measurement of kinship and so thrown new light on mating systems (Spaulding 2007) and population dynamics (above).

Taxonomy has become crucial to conservation practice because red data lists, based on taxonomy, are used to identify conservation priorities. Most red data books list species (e.g. IUCN 2010), and red-listed species receive particular attention. Therefore, it makes a difference if a population of grouse is considered a distinct species. In this context, future genetic studies may help to identify units of evolutionary significance, and thus find more objective criteria for conservation priorities.

Landscape ecology

The spatial structure of habitats and populations has become a major topic in grouse research (Storch 2000). Understanding the effects of the large-scale clear-cutting and fragmentation of boreal forests that has occurred since the 1970s, for example, has demanded larger-scale approaches to wildlife ecology (Bissonette & Storch 2002).

Dispersal among habitat patches may be important for the persistence of fragmented populations. Thus, metapopulation theory tells us that small populations in isolated habitat patches may be more vulnerable to demographic accidents, while conservation genetics warns that small populations may suffer from inbreeding depression (Westemeier et al. 1998).

Valuable information about individuals' movements can be gained by telemetry, but radio-tags may alter a bird's behaviour (Caizergues & Ellison 1998), and workers should be aware of this possibility. Also, catching and radio-tagging enough birds to characterise complex dispersal patterns in spatially structured populations is often impracticable, particularly in threatened, low density populations. Alternatively, the distribution of DNA variants in such populations is used indirectly to infer dispersal patterns, habitat connectivity and population viability (Segelbacher 2008). This can have major implications for conservation, especially of fragmented populations.

DNA-based inferences about population structure and movement have often assumed that the DNA sampled during a short period represents the current distribution of genotypes. The demonstration that the spatial structure of red grouse genotypes changed rapidly from one year to the next, in an area $< 1\ km^2$ (Piertney et al. 2008), suggests that such assumptions should be re-evaluated. We anticipate that further dialogue between ecologists and geneticists will lead to better models and sampling procedures for inferring grouse dispersal patterns from the geographical distribution of their DNA variants.

Diet

Grouse have a remarkable digestive system adapted to coarse foods (Watson & Moss 2008), although far more attention has been paid to what they eat than to how they process it. However, the topic of diet, plainly important to grouse, has shown a spectacular decline in popularity (see Table 4). The diets of most grouse species have frequently been described via standard analyses of crop contents or faeces. The general patterns are well-known, and further merely descriptive accounts of the food composition of adult grouse would be difficult to publish in peer-reviewed international journals.

Yet, there are gaps in existing knowledge. Selection of insect food by grouse chicks is poorly understood and of potential significance for conservation, particularly because so much land has been drained for crops and so made less suitable for the arthropods eaten by grouse chicks. Such studies are lacking, partly because it is no longer regarded as ethical to kill chicks for their crop contents. The alternative approach of faecal analysis is time-consuming and tends to be biased towards recording food items with hard, indigestible parts (Picozzi et al. 1999). Perhaps this topic will be tackled more frequently as DNA-based methods of analysing faecal contents become more reliable (Prugh et al. 2008).

Envoi

Fundamental descriptive studies on population biology, behaviour, diet and habitat have been done for most species of grouse. Answers to many difficult questions awaited improvements in methods including statistics, telemetry, DNA technology and GIS systems. The funding environment has changed, so that detailed long-term academic population studies are now less common and aspects of conservation biology, which are shorter and easier to justify, have come to the fore.

The topics of pollution, climate change and human disturbance, all consequences of increased human impact, received few hits (see Table 4). They will inevitably receive more attention. If we are to retain grouse populations in the face of such challenges, our understanding of habitats must get beyond mere description, and incorporate the genetic, demographic and spatial processes that sustain grouse. This will involve learning more about how birds adapt to modified and managed habitats, and how to design grouse sanctuaries. Integrating the use of land by people for recreation, and by grouse for survival, will mean finding out more about what does, and what does not, disturb or stress grouse.

Grouse sanctuaries, however, will need sound justification. There is evidence that grouse are good umbrella species (Suter et al. 2002, Pakkala et al. 2003), and therefore good grouse management should benefit many other less charismatic species and their habitats. As umbrella species, grouse would stand for an entire community, and so be much more likely to get political support for their conservation.

When large predators, such as lynx *Lynx lynx*, coyote *Canis latrans* or wolf *Canis lupus*, are reduced or exterminated, it seems that smaller predators, such as red foxes *Vulpes vulpes*, become more abundant and increasingly affect grouse populations (Lindström et al. 1994, Mezquida et al. 2006). This is partly because larger predators are typically sparser and have less impact on grouse numbers, and partly because they may kill significant numbers of smaller predators. This principle, of mesopredator release, might be used to reduce the effects of predation on grouse populations, perhaps by sparing larger predators from persecution and allowing them to suppress mesopredators. Of course, in major parts of the grouse range, humans will not accept large carnivore recovery as a conservation measure; yet, we believe that predation and the way predator-prey relationships are determined by human land use and other activities are key to understanding grouse populations.

Storch (2000) made two points that remain valid. First, as in ecology generally, increasing integration of disciplines is resulting in broader syntheses, both geographically as in landscape ecology (above) and conceptually as, for example, population genetics informs population dynamics (Moss et al. 2003). Second, there is insufficient documentation of grouse conservation and management. Although our results showed increasing numbers of publications on 'conservation' and 'management', these papers in peer-reviewed journals typically provided scientific guidelines for managers to build on, rather than reporting the outcome of management actions. Little is published on techniques, successes and failures, or on management experiments, despite the fact that such work is being done.

Despite this shortcoming, the scientific basis for conservation seems much better for grouse than for most other galliformes. Indeed, the large collective expertise in grouse biology and conservation within the IUCN/SSC WPA Galliformes Specialist Group (available at: http://www.iucn.org/about/work/programmes/species/about_ssc/specialist_groups/) could provide useful guidelines for less well-understood, threatened galliformes taxa. Thus, we strongly encourage systematic reviews on grouse conservation biology and management, which could be valuable guidance for conservation practitioners worldwide.

We anticipate that the current emphasis on conservation in grouse research will continue, with improved genetic techniques allied with GIS for determining dispersal patterns, habitat structure and population viability and dynamics. The management of grouse and their habitats should involve better understanding of these processes, and of how the birds survive in an ever-changing environment.

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