Received: 13 September 2017 | Accepted: 13 December 2017

DOI: 10.1111/1365-2664.13128

RESEARCH ARTICLE

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

Regulation of body reserves in a hunted wader: Implications for cold-weather shooting restrictions

Carlos Sánchez-García[1] | Owen Williams[2] | Andrew Hoodless[1]

[1]Game & Wildlife Conservation Trust, Fordingbridge, UK

[2]Woodcock Network, Aberystwyth, UK

Correspondence
Carlos Sánchez-García
Email: investigacion@fundacionartemisan.com

Present address
Carlos Sánchez-García, Fundación Artemisan, Ciudad Real, Spain

Funding information
the Game & Wildlife Conservation Trust

Handling Editor: Gavin Siriwardena

Abstract

1. Severe winter weather can reduce avian energetic reserves. At such times, reducing disturbance, and therefore energy expenditure, through science-based policy is crucial to mitigating negative impacts on survival.
2. We used allometric equations to examine the energy reserves of Eurasian woodcock *Scolopax rusticola*, a popular quarry species across most of Europe, in relation to time of winter, location and temperature. We used data from 221 dissected birds, shot in Britain in two winters (2013/14, 2014/15), and 1,689 live birds captured during six consecutive winters (2010/11 to 2015/16).
3. Woodcock are able to store large amounts of energy as fat in mid-winter and increase energy reserves as night air temperature drops to below 0°C, provided the ground thaws during the day.
4. In the event of cold weather in Britain, the mean potential flight distance of woodcock, based on mobilizable energy estimates of shot birds, is 860 km. If they do not move away, woodcock could withstand frozen conditions without feeding for a mean of 6 days.
5. *Synthesis and applications*. To reduce the effects of cold weather on Eurasian woodcock *S. rusticola*, shooting should be restricted before energy reserves are depleted. Current policies vary across Europe, but our results suggest that restrictions should come into force sooner, after 4 days of continually frozen ground at inland sites. Restrictions should cover large regions and remain in operation for 7 days after the end of the cold spell.

KEYWORDS

Britain, energetics, fasting endurance, hunting restrictions, ringing, *Scolopax rusticola*, shooting, woodcock

1 | INTRODUCTION

Severe winter weather can place a strain on avian energetic resources (Newton, 1998). Virtually all birds face a daily trade-off between starvation and predation during winter: carry too little fat (energy) and they risk starving, carry too much fat and they reduce the speed of their escape response from predators (Bednekoff & Houston, 1994; Gosler, Greenwood, & Perrins, 1995). This trade-off is influenced by the predictability of food sources (Lima, 1986). There is a lack of studies dealing with the effects of severe weather events on the regulation of energy reserves, and also with the indirect and additive effects of human activity on the survival of species during winter (including hunting) (Ferrand, Aubry, Landry, & Priol, 2013).

This is the case for the Eurasian woodcock *Scolopax rusticola* L. (hereafter woodcock), a widespread woodland specialist (Hoodless, 1995) and long-distance migrant, which leaves its breeding grounds in Scandinavia, Finland, the Baltic States and Russia for wintering areas in southern and western Europe in autumn (Hoodless et al., 2013;

FIGURE 1 Map of Britain showing the four regions from which samples of shot woodcock were obtained and the two ringing sites where live woodcock were captured (1 mid-Wales, 2 Hampshire)

Thorup, 2006). It is widely hunted throughout its European wintering areas, with around 2.3–3.5 million birds shot per year, mainly in France, Italy, Britain, Ireland and Spain (Guzmán & Arroyo, 2015; Lutz & Jensen, 2006).

In Europe, the woodcock is categorized as a species of "Least Concern" (Birdlife International, 2017), though there is evidence for declines in breeding numbers and range in Britain and Switzerland, probably owing to changes in woodland structure, intensification of agricultural practices and human disturbance (Estoppey, 2001; Heward et al., 2015). The species has been recently "Red listed" as a bird of conservation concern in the United Kingdom (Eaton et al., 2015). Additionally, it has been demonstrated that shooting may be additive to natural mortality and affect population growth rate (Duriez, Eraud, Barbraud, & Ferrand, 2005; Péron et al., 2012), at a time when woodcock are susceptible to severe winter weather (Tavecchia et al., 2002).

To reduce the disturbance impact of shooting gamebirds under stress during cold spells, some European countries impose restrictions during these periods. In France, cold spells are defined as periods of at least 6–7 consecutive days when daily temperatures are 10°C below the seasonal average, minimum daily temperatures are below −5°C and maximum daily temperatures prevent thawing (MEDDTL, 2010). In Spain, shooting is banned when snow covers the ground (Agencia Estatal Boletín Oficial del Estado, 2015). In Great Britain, voluntary restraint in the shooting of wildfowl and waders is recommended after seven consecutive days of frozen conditions (determined as minimum daily air temperature <1°C and minimum daily grass temperature <−2°C) are recorded at more than half of a network of 25 coastal meteorological stations, although statutory suspension does not come into force until day 15. A "Protection Order" of 14 days is then enforced, although it can be revised after 7 days (Ellis, 2012).

These measures are largely based on "best guesses" and in Britain are designed to protect a range of geese, ducks and waders (Stroud et al., 2006). Despite evidence of elevated mortality in prolonged cold weather, the relationships between the duration of cold spells, energy expenditure and mortality are poorly documented for most species (Davidson & Clark, 1985; Davidson & Evans, 1982). In addition, the effect of cold weather on energy expenditure in woodcock may differ from that on coastal waders because the woodcock is found largely inland, where temperatures are typically lower than at the coast but where it might benefit from reduced exposure by feeding in woodland (Hoodless, 1995).

The aim of this study was to examine variation in energy reserves, and hence the potential fasting endurance or escape flight distance, of woodcock during the winter and in relation to location and temperature. Because woodcock feed predominantly on soil invertebrates, particularly earthworms and leatherjackets in winter (Granval, 1987), food abundance is unlikely to ever be limiting. Consequently, we hypothesize that woodcock should be able to increase energy reserves at reduced temperatures until a threshold when access to food is limited because the invertebrates remain too deep or woodcock are prevented from probing. We use data from dissected birds, shot in winter, to examine individual variation in fat stores and the relationship between fat levels and body weight. We use data from live-captured birds to assess changes in mobilizable energy in relation to season and weather. We discuss the implications for the suspension of hunting in cold weather.

2 | MATERIALS AND METHODS

2.1 | Carcass dissection

A total of 221 woodcock collected from hunters during the winters of 2013/14 ($n = 77$) and 2014/15 ($n = 144$) were dissected. Birds were shot from early December to late January in four regions (Figure 1): Cornwall (pastoral land), Wessex (mixed farmland), East Anglia (predominantly arable farmland) and Scotland (mixed farmland). In 2013/14, 72 of the samples were from Cornwall but in 2014/15 sample sizes were Cornwall 42, Wessex 13, East Anglia 50 and Scotland 39. Shooting did not coincide with the main migration periods of foreign woodcock, which represent the majority of birds in winter (Hoodless & Coulson, 1994; Hoodless et al., 2013).

Carcasses were individually placed in labelled polythene bags and were frozen at −20°C within 10 hr of shooting. Six birds were dissected from fresh. After defrosting at 10–12°C for 1 day, birds were weighed (±0.01 g) and wing length (maximum flattened chord ± 1 mm) was measured. Birds were sexed by dissection (except one bird from Scotland) and aged by plumage characteristics of the wing, being classified as first-winter birds (<1 year old) or adults (>1 year old) (Ferrand & Gossmann, 2009). Birds were plucked and the abdominal fat and intestinal fat were dissected and weighed (hereafter referred to as dissected fat). The major and minor pectoral muscles were divided longitudinally along the sternum and the right half of these muscles was removed and weighed. This value was multiplied by two to obtain the total pectoral muscle mass. In four birds, pectoral mass could not be measured owing to shot damage.

2.2 | Capture of live birds

We caught woodcock at night from November to March, using a spot-lighting technique (Gossmann, Ferrand, Loidon, & Sardet, 1988), during the period 2010/11 to 2015/16, at one site supporting wintering immigrant woodcock (Ceredigion, mid-Wales) and a site with mainly immigrants and some resident birds (Hampshire) (Hoodless, Lang, Aebischer, Fuller, & Ewald, 2009) (Figure 1). Birds were aged, ringed and weighed (±0.1 g), and wing length was measured (±1 mm). Woodcock were not sexed as current morphometric methods are not capable of separating all birds, and the measures required for the method with greatest discriminatory power, separating up to 79% of birds, were not practical for when working alone at night (Aradis, Landucci, Tagliavia, & Bultrini, 2015; Ferrand & Gossmann, 2009). We were not able to sex birds using molecular techniques. Effects of variables on energy reserves were examined for 549 woodcock captured in Hampshire and 1,140 in Wales (Table S1). Data for birds recaptured within 30 days were excluded to avoid pseudo-replication.

2.3 | Energy reserves and functional parameters

Total dry fat mass and dry protein mass were calculated from the fresh mass of abdominal and intestinal fat and from the fresh mass of pectoral muscles, respectively, for shot birds and from fresh weight for live-captured birds, using allometric equations developed by Boos (2000) (Table S2). Mobilizable energy (ME), the energy (kJ) available when fasting in cold weather or for flying to milder areas, was estimated by multiplying the total dry fat and protein masses, minus the fat and protein remaining on woodcock starved to death during cold spells (Boos, 2000), by their caloric densities (39.6 kJ/g for dry fat and 18.0 kJ/g for dry protein, Jenni & Jenni-Eiermann, 1998). Potential fasting endurance and escape flight distance were estimated from ME and standard calculations of basal metabolic rate and energy expenditure (Table S2). Estimation of fasting endurance followed the method of Boos (2000), involving daily recalculation of energy expenditure by fasting birds, taking into account the daily loss of body mass and the masses of fat and protein catabolized for energy production per day.

2.4 | Weather data

Temperature data were obtained from weather stations <15 km from sites where birds were shot or ringed (http://www.wunderground.com). We expected small local differences in temperature between shooting or ringing sites and weather stations to add noise to relationships rather than bias results. Because woodcock feed mainly at night in open habitats in winter (Duriez, Fritz, Binet, Tremblay, & Ferrand, 2005), we were interested in the effect of mean night temperature and wind chill index (determined from dusk and dawn times) on woodcock weights and ME levels. We extracted data for 7 days before shooting or before birds were captured, based on typical rates of potential body weight increase in other waders. Mean night temperature and night wind chill index were correlated and so we used temperature in analyses, as recommendations based on the results are easier to implement.

To examine changes in ME during and after cold spells, we used data on live-captured woodcock and identified days of freezing as those when the minimum daily temperature was below 0°C at the ringing sites. If two consecutive cold spells were separated by ≤3 days, they were considered as the same one. This follows the procedure for counting frozen days up to the implementation of the UK “Protection Order” and observations during the 2010/11 British cold spell were that the ground was only starting to thaw after 2 days, with temperatures of +3°C and +5°C (Prior & Kendon, 2011). We distinguished three catching periods in relation to cold spells: “before” (captures 1–5 days before the onset of the cold spell), “during” and “after” (captures 1–5 days after the cold spell). We identified 17 cold spells during 2010/11–2015/16 when we had captured woodcock during the period from 5 days before to 5 days after the freezing weather. To increase the sample size, we included data from two cold spells, in 2008/09 and 2009/10, at the Welsh ringing site. Mean cold spell duration was 7.3 ± 1.0 days (±*SE*), and mean minimum daily temperature during cold spells was −2.7 ± 0.3°C (±*SE*) (Table S3).

To examine cold spells across the main European wintering areas for woodcock, we extracted temperature data during November–January 2007/08–2016/17 for three inland weather stations within each of five areas (http://www.wunderground.com, Table S4). We identified periods when minimum temperature was ≤−2°C for ≥7 days, minimum and maximum temperatures were ≤−2°C and ≤3°C for ≥4 days, and minimum and maximum temperatures were ≤−5°C and ≤3°C for ≥4 days. One day of thaw with higher temperatures was permitted, but not counted, for all periods.

2.5 | Statistical analysis

We found a difference in the wing length of woodcock between age classes (adults 2.2 mm longer than first-winter birds) and sexes (males 2.2 mm longer than females) of shot birds (analysis of variance (ANOVA) age $F_{1,217}$ = 9.89, p = .002, sex $F_{1,217}$ = 9.69, p = .002, age × sex $F_{1,216}$ = 0.07, p = .788). There was a similar difference in the wing length of live-captured adults and first-year birds

($F_{1,1687}$ = 33.08, p < .001). Using wing length as a proxy for structural size, we, therefore, corrected all fresh weights and ME values using the overall mean wing length of 201 mm (new value = old value × (201/wing length)) to reduce variation and ensure that any differences between ages and sexes were attributable to behavioural or physiological differences.

Data for shot birds were pooled for the two winters as the majority of the 2013/14 sample was from Cornwall, and there were no differences in fresh weight, dissected fat mass, pectoral mass or ME of Cornish birds between winters (Table S5). In shot birds, we used ANOVA to examine the effects of bird age, sex and sampling region on fresh weight, dissected fat mass, pectoral mass and ME. Similarly, we used ANOVA to examine the effects of age, month, winter and ringing site on ME of live-captured birds. All interactions were tested in the full models and non-significant interactions were dropped by orders to produce reduced models.

General linear models (GLM) with ME as the dependent variable were used to examine relationships with mean night temperature prior to the shooting or capture of woodcock. Bird age and region (for shot birds) or ringing site (live-captured birds) were included along with the interactions temperature × age and temperature × region/ringing site. Non-significant interaction terms were dropped in order of significance from the full model to produce a reduced model consisting of structural variables and significant interaction terms.

To examine changes in ME during cold spells, we first performed an ANOVA with catching period, bird age and ringing site as factors and tested all interactions. Then, for captures during cold spells, we used a GLM with ME as the dependent variable to examine relationships with days since the start of the cold spell (hereafter cold spell days) and lowest night temperature. The full model included bird age and ringing site, their interactions with cold spell days and lowest temperature and the interaction cold spell days × lowest temperature. Non-significant interaction terms were dropped sequentially to produce a reduced model with main effects and significant interaction terms.

All statistics were calculated in GENSTAT v18.1 (VSN International, Hemel Hempstead, UK). Residuals were checked for normality and homoscedasticity of variances.

3 | RESULTS

3.1 | Variation in body weight, dissected fat mass and pectoral mass

In shot birds, fresh weight was correlated with dissected fat mass (n = 221, r = .68, p < .001) and the sum of dissected fat and pectoral mass (n = 217, r = .71, p < .001). Dissected fat mass was weakly correlated with pectoral mass (n = 217, r = .33, p < .001). Region had the largest effects on fresh weight and dissected fat mass (Table 1). Higher mean regional values of fresh weight and dissected fat mass corresponded with lower mean region temperature for December and January (Scotland 3.0°C, East Anglia 4.2°C, Wessex 4.9°C, Cornwall 7.3°C, source: www.metoffice.gov.uk/public/weather/climate). Male woodcock were lower in weight than females, owing to smaller pectoral muscle mass rather than a difference in fat mass. Bird age only affected fat mass, with adults carrying more fat than first-winter birds.

3.2 | Mobilizable energy, fasting endurance and flight distance

For all shot birds, the contribution of fat to ME ranged from 68% for fresh weights of 231–250 g to 82% for weights of >371 g (Figure 2). Among shot birds, adults had higher ME values than first-winter birds (Table 2), although the difference was small (Table 3).

TABLE 1 ANOVA model estimates and significance for effects of bird age, sex and region on fresh weight, dissected fat and total pectoral mass of woodcock shot in December–January 2013/14 and 2014/15. First- and second-order interactions were not significant and were removed from final models

		Fresh weight (g)			Dissected fat (g)			Pectoral mass (g)		
Factor	Level	Estimate	*SE*		Estimate	*SE*		Estimate	*SE*	
	Constant	325.26	3.55		5.471	0.432		84.86	1.10	
Age	First-winter	−0.09	3.11		−0.889	0.378		−1.86	0.96	
Sex	Male	−11.51	2.97		−0.079	0.361		−2.62	0.92	
Region	Cornwall	−28.50	3.79		−2.805	0.461		−2.86	1.18	
	Wessex	−4.48	6.63		−0.393	0.806		1.18	2.10	
	Scotland	5.04	4.62		0.926	0.561		−1.39	1.43	
		df	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Age		1,214	0.00	.976	1,214	5.52	.020*	1,210	3.72	.055
Sex		1,214	15.04	<.001***	1,214	0.05	.827	1,210	8.11	.005**
Region		3,214	33.00	<.001***	3,214	25.01	<.001***	3,210	2.82	.040*

Model reference levels were adult, female and East Anglia.
Significance *p < .05, **p < .01, ***p < .001.

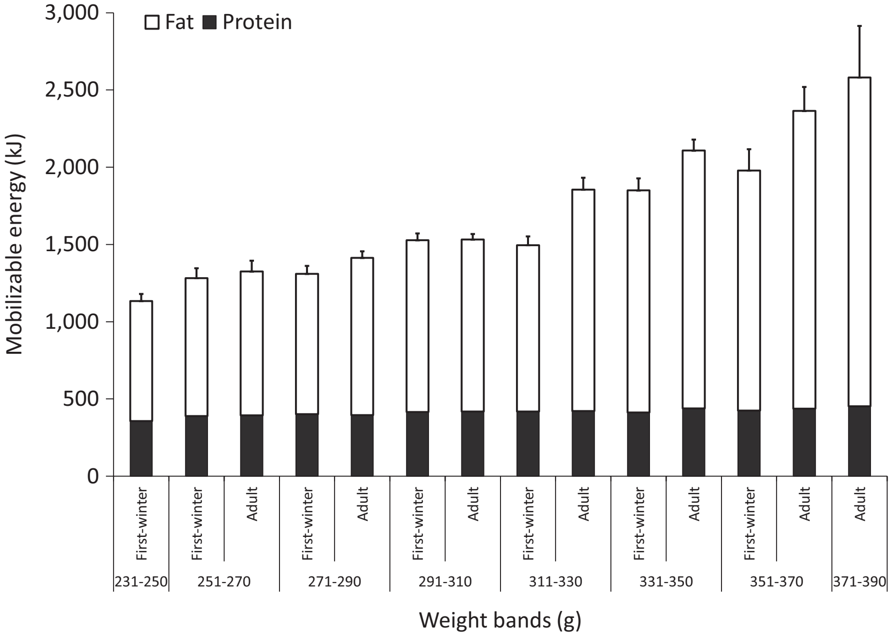

FIGURE 2 Mean (+*SE*) mobilizable energy from dissected fat and pectoral mass by age class, within eight fresh weight bands

TABLE 2 ANOVA model estimates and significance for effects of bird age, sex and region on the mobilizable energy (kJ) of shot woodcock and for effects of bird age, ringing site, month and winter on mobilizable energy of live-captured woodcock in winters 2010/11 to 2015/16. Second- and third-order interactions were not significant and were removed from final models along with non-significant first-order interactions. The effects of month and winter on mobilizable energy of live-captured birds are presented in Figure 4

Birds	Factor	Level	Estimate	*SE*	*df*	*F*	*p*
Shot		Constant	1844.3	56.4			
	Age	First winter	−120.7	49.3	1,210	6.00	.015*
	Sex	Male	−7.4	47.1	1,210	0.02	.875
	Region				3,210	23.41	<.001***
Live captured		Constant	2463.9	63.7			
	Age	First winter	−89.6	22.8	1,1656	15.45	<.001***
	Ringing site	Hampshire	31.3	26.5	1,1656	1.39	.238
	Month				4,1656	16.40	<.001***
	Winter				5,1656	3.86	.002**
	Month × Winter				20,1656	4.71	<.001***

Reference levels were adult, female and East Anglia and mid-Wales.
Significance *p < .05, **p < .01, ***p < .001.

Consequently, adults were only able to survive 0.8 days longer, or fly around 95 km further, on average, than first-winter birds. Woodcock in Cornwall had significantly lower ME values than birds from the other three regions (Tables 2 and 3). All birds were able to fast for at least 3 days, and fasting endurances were (mean ± *SE*) 5.0 ± 0.1 days for Cornish birds and 6.4 ± 0.2 days for birds from the other regions (Figure 3). Alternatively, all birds were able to make escape flights of at least 600 km, and Cornish birds could have made escape flights of (mean ± *SE*) 781 ± 11 km, compared with 941 ± 19 km for birds from other regions (Figure 3).

Among live-captured woodcock, adults had higher mean ME than first-winter birds (Tables 2 and 3). Mobilizable energy varied between months and across winters (Table 2). Mean ME was similar among woodcock caught in Hampshire and in mid-Wales, and two peaks in ME were recorded at both sites: one in December–January and the other in March (Table 2, Figure 4). If woodcock do not move with the onset of cold weather and endure continuous frozen conditions without feeding for 4 days, 80% of shot birds and 93% of live birds may survive, but if they fast for 7 days, only 9.5% (shot birds) to 22% (live-captured birds) may survive.

3.3 | Effects of temperature on mobilizable energy

For shot birds with known shooting date (Table S6), we found no relationship between ME and mean night temperature for the preceding seven nights when region was included in the GLM (Table 4). However, temperatures were partially confounded with region,

TABLE 3 Means (±*SE*) of mobilizable energy, flight distance and fasting endurance for shot and live-captured woodcock in relation to age and region. Ranges for flight distance and fasting endurance are in brackets

Sample	Factor	Level	*n*	Mobilizable energy (kJ)	Flight distance (km)	Fasting endurance (days)
Shot	Age	Adult	129	1,708 ± 39	897 ± 17 (620–1,706)	6.0 ± 0.1 (4–14)
		First winter	88	1,497 ± 32	802 ± 13 (608–1,176)	5.2 ± 0.1 (3–8)
	Region	Cornwall	112	1,417 ± 23	781 ± 11 (613–1,176)	5.0 ± 0.1 (3–8)
		Wessex	13	1,757 ± 124	905 ± 52 (621–1,295)	6.2 ± 0.4 (4–9)
		East Anglia	50	1,811 ± 51	931 ± 23 (655–1,344)	6.2 ± 0.2 (4–9)
		Scotland	42	1,902 ± 79	964 ± 35 (608–1,706)	6.7 ± 0.3 (3–14)
Live captured	Age	Adult	749	2,042 ± 18	1,024 ± 7 (345–1,486)	6.6 ± 0.1 (2–10)
		First winter	940	1,942 ± 16	984 ± 6 (332–1,890)	6.3 ± 0.1 (1–12)

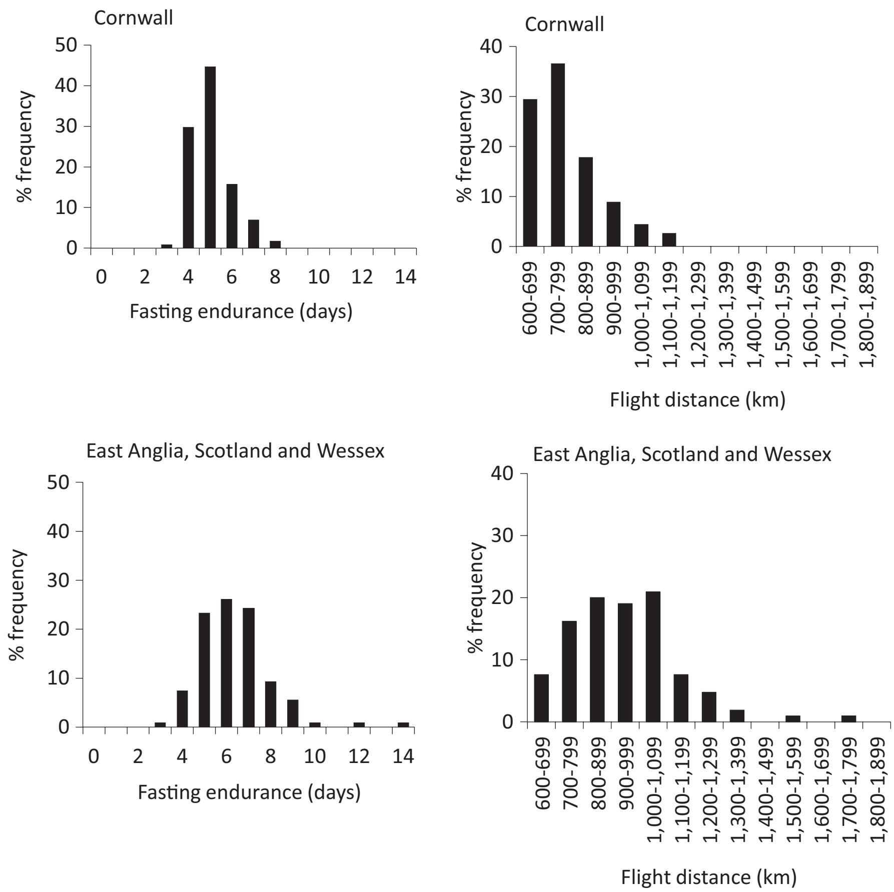

FIGURE 3 Variation in fasting endurance and flight distance in woodcock shot in Cornwall and East Anglia, Scotland and Wessex

such that there was a difference in mean values and the range for Cornwall was almost exclusive of the ranges for the other regions (Table S7). With region excluded from the model, we found a negative relationship across the range of temperatures +0.4 to +9.3°C (Table 4). For live-captured woodcock, ME was negatively related to mean temperature during the previous seven nights within the range −1.0 to +13.2°C (Table 4).

The effect of cold spells on ME levels of live-captured woodcock was small, with a 6.7% drop in ME during cold spells relative to the 5 days before they started (mean ± *SE*; before 2,142 ± 51 kJ (n = 89), during 1,998 ± 63 kJ (n = 60), after 2,095 ± 52 kJ (n = 88)). There was no difference in ME between catching periods (catching period $F_{1,232}$ = 1.57, p = .210, bird age $F_{1,232}$ = 4.22, p = .041, ringing site $F_{1,232}$ = 3.12, p = .079, interactions not significant; see Figure S1 for detail of variation in ME).

During cold spells, we found a weak interaction effect between cold spell days and the lowest temperature on ME, indicating that ME was lower during longer, colder periods (Table 5). There were also weak interactions between bird age and lowest temperature and between cold spell days and ringing site (Table 5). Between −2°C

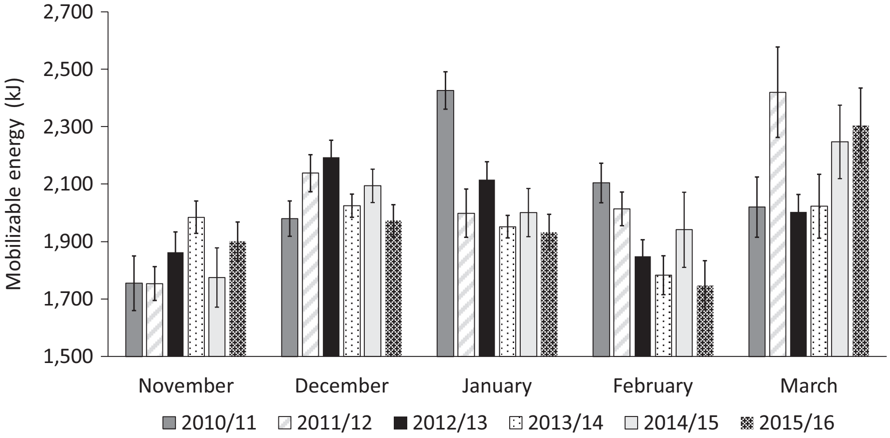

FIGURE 4 Mean (±*SE*) mobilizable energy of live-captured birds ringed in Hampshire and mid-Wales

TABLE 4 GLM model estimates and significance for effects of mean night-time temperature, during the previous seven nights, on the mobilizable energy (kJ) of (a) shot woodcock (with known shooting date, *n* = 140), including region, and (b) excluding region, and (c) of live-captured woodcock (winters 2010/11 to 2015/16, excluding March). Results are presented for full models, with parameters in italics dropped from final models

Birds	Parameter	Level	Estimate	*SE*	*df*	*F*	*p*
(a) Shot		Constant	1,745	124			
	Temperature		23	27	1,130	0.73	.394
	Age	First-winter	−121	70	1,130	3.00	.086
	Region				3,130	7.22	<.001***
	Temperature × Age				*1,126*	*0.60*	*.441*
	Temperature × Region				*3,126*	*1.76*	*.158*
(b) Shot		Constant	2,091	105			
	Temperature		−63	19	1,135	10.92	.001**
	Age	First-winter	−144	74	1,135	3.80	.053
	Temperature × Age				*1,132*	*0.01*	*.943*
(c) Live captured		Constant	2,201	34			
	Temperature		−29	4.4	1,1558	44.31	<.001***
	Age	First-winter	−83	24	1,1558	11.97	<.001***
	Ringing site	Hampshire	55	26	1,1558	4.66	.031*
	Temperature × Age				*1,1556*	*2.93*	*.087*
	Temperature × Ringing site				*1,1556*	*0.03*	*.865*

Reference levels were adult, East Anglia (shot birds) and mid-Wales (live-captured woodcock).
Significance $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$.

and −8°C, adults were better able to maintain their energy reserves than first-winter birds (Figure S2). In the case of days since start of the cold spell, we observed a strong negative relationship between ME and cold spell days in Hampshire, but no significant relationship in Wales (Figure S2).

3.4 | Cold spells across woodcock wintering areas

Cold spells were infrequent during the 10 years 2007/08 to 2016/17, mainly occurring in two winters (2009/10 and 2010/11). Numbers of cold periods did not vary appreciably between countries but durations were typically longer in Scotland and England than in France, Spain or Italy (Table 6). Maximum temperature during cold spells was lower in Scotland and England than in the other regions (Table 6).

4 | DISCUSSION

Woodcock stored high amounts of energy in winter as fat, which agrees with a previous study conducted in France (Boos, Boidot, & Robin, 2005). Literature on waders in the northern hemisphere indicates that many species regulate their body mass seasonally and in relation to short-term fluctuations in temperature. As frost reduces the ability of woodcock to probe the soil and capture earthworms,

TABLE 5 GLM model estimates and significance for effects of cold spell days and lowest minimum temperature during cold spells on the mobilizable energy (kJ) of live-captured woodcock. Results are presented for the full model, with parameters in italics dropped from the final model

Parameter	Level	Estimate	*SE*	$t_{(52)}$	*p*
	Constant	1,716	295	5.81	<.001***
Age	First winter	522	246	2.12	.039*
Ringing site	Hampshire	570	238	2.40	.020*
Cold spell days		−124	62	−2.02	.048*
Lowest temperature		−2	51	−0.05	.963
Age × Lowest temperature		141	53	2.68	.010*
Ringing site × Cold spell days		−121	56	−2.15	.037*
Cold spell days × Lowest temperature		−35	13	−2.59	.013*
Age × Cold spell days		*−20*	*31*	*−0.62*	*.537*
Ringing site × Lowest temperature		*−107*	*115*	*−0.93*	*.354*

Reference levels were adult and mid-Wales.
Significance **p* < .05, ***p* < .01, ****p* < .001.

TABLE 6 Mean numbers of cold periods meeting different criteria during November–January 2007/08–2016/17 and mean durations (days ± *SE*) of those periods. Also presented is the mean maximum temperature for days when minimum temperature was below −2°. GLM results for duration of cold periods are from a model that also included winter as a factor. In the GLM model for maximum temperature, minimum temperature was included as a covariate (mean −4.6°C)

	Periods ≥ 7 days min. −2°C		Periods ≥ 4 days min. −2°C, no thaw		Periods ≥ 4 days min. −5°C, no thaw		
Area	*n*	Duration	*n*	Duration	*n*	Duration	Mean max. temperature (°C) when min. = −4.6°C
Scotland (central)	5.3	14.4 ± 1.8	6.0	9.6 ± 1.7	3.7	10.7 ± 1.9	2.8 ± 0.2
England (central)	3.0	11.3 ± 0.8	4.7	8.7 ± 0.9	1.7	5.8 ± 0.4	1.0 ± 0.3
France (north-west)	3.0	9.0 ± 0.4	4.3	5.4 ± 0.4	1.0	5.0 ± 0.6	3.7 ± 0.3
Spain (north)	6.3	10.0 ± 0.7	3.0	5.4 ± 0.4	1.0	4.7 ± 0.3	5.6 ± 0.2
Italy (north)	5.3	10.8 ± 1.3	5.3	5.2 ± 0.3	2.0	4.7 ± 0.2	4.3 ± 0.2
		$F_{4,55} = 3.11$		$F_{4,56} = 5.74$		$F_{4,19} = 2.89$	$F_{4,924} = 77.23$
		$p = .022$*		$p < .001$***		$p = .050$	$p < .001$***

their most important prey (Granval, 1987; MacDonald, 1983), it seems plausible that falling temperature triggers greater energy storage to meet the increased thermoregulatory demand and as a precaution against starvation. This most likely explains the higher energy values in shot woodcock from Wessex, East Anglia, and Scotland compared with birds from Cornwall, and the first peak in energy storage observed in live-captured birds in December–January.

Woodcock should be able regulate energy reserves efficiently when the ground is not frozen because they can shelter in woodland by day and reduce energy expenditure, as wind has less of an exposure effect than on coastal waders (Mitchell, Scott, & Evans, 2000). A radio-tracking study employing tilt-switch activity transmitters found that woodcock only needed to feed for 3.5–5.0 hr per day in mild conditions, when able to feed on fields at night, to satisfy their daily energy need (Duriez, Fritz, et al., 2005). Although feeding areas inland are likely to freeze before those at the coast, woodcock may still have the option of feeding in woodland or beside unfrozen streams during the day when the ground freezes at night. Feeding in woodland is not likely to deliver the same energy intake per unit time, owing to lower food availability than in fields (Hoodless & Hirons, 2007), but the temperature will probably need to be sufficiently low to keep the ground frozen for a substantial part of the day before woodcock start to be impacted.

Once permanently frozen conditions set in, our data suggest that there is the potential for woodcock to starve to death within a week. In France, it is known that cold spells increase woodcock mortality (Gossmann & Ferrand, 1998; Lormée et al., 2013; Péron et al., 2011). The temperature inland is, on average, 3°C lower than at the coast (www.metoffice.gov.uk). So a day counted as frozen at the coast under the UK statutory cold-weather suspension system (minimum air temperature below 1°C) will typically equate to a minimum daily temperature below −2°C inland. Mean daily minimum temperature during the cold spells for which we have data was −2.7°C, and mean mobilizable energy reserve during these periods was still 1,998 ± 63 kJ, compared with the mean estimate at starvation of

780 kJ. Our data, therefore, suggest that woodcock were able to cope adequately with these temperatures.

Examination of our cold spell data indicated that a minimum daily temperature of −2°C equated to a mean daily temperature of +2°C, suggesting that the ground was sufficiently thawed for long enough in the day for woodcock to almost maintain their energy levels. Measures of soil penetrability indicate that grass fields start to become too hard for woodcock to probe below −2.5° and cereal fields and stubbles are impenetrable at this temperature (A. Hoodless, *unpubl. data*). Under the conditions experienced in the cold spells which we monitored, our data suggest that after 7 days of cold weather, the trigger for "voluntary restraint" in shooting under the UK system, woodcock would have lost on average 33 g fresh weight and after 15 days, the point at which a statutory suspension of shooting would come into force, they would have lost on average 70 g. At this time mean woodcock weight would have dropped to about 255 g and birds would have about 1,428 kJ mobilizable energy. Lower temperatures than those encountered in our study would impact woodcock reserves more rapidly, and minimum temperatures below −5°C would prevent the ground thawing during the day and prevent woodcock feeding in Scotland and England (Table 6). The effects on woodcock documented during cold spells in France occurred when minimum daily temperatures were below −5°C (Gossmann & Ferrand, 1998; Lormée et al., 2013). Our data suggest that first-winter woodcock may be affected disproportionately if cold spells involve very low temperatures.

Studies are needed on the behaviour of woodcock at the onset of cold spells, to understand conditions under which they are unable to feed. We know that some woodcock move from their regular winter sites when daytime temperatures fall below 3°C, as recorded in Hampshire with the departure of radio-tagged birds in January 2009, December 2009 and January 2010 (Powell, 2012). One of these birds was recovered *c*. 100 km to the south-west shortly after departure. In this study, resident woodcock (determined from stable-isotope analysis) remained on site throughout the cold spells, while migrants largely departed (Powell, 2012). Hence, shooting during these periods would have had a disproportionate impact on local breeders. As shown in Eurasian cranes after an extreme flooding event in Britain (*Grus grus*) (Soriano-Redondo et al., 2016), it is unlikely that woodcock populations would collapse in a single year, and woodcock hunting disturbance may be low owing to the nocturnal behaviour of the species (Ferrand et al., 2013). But indirect effects resulting from movements to avoid severe weather conditions may occur owing to the increased energy expenditure and predation risk (including hunting) at the new wintering sites. Some of the relatively new technologies now available for smaller birds, such as GPS tags and accelerometers, could be used to improve our knowledge of woodcock behaviour during cold weather.

Although the British cold-weather shooting policy is broadly appropriate for protecting woodcock, there is potential for substantial mortality before the triggering of "voluntary restraint" or the statutory suspension of hunting if weather conditions result in continuous frozen ground, because the species' mean fasting endurance is 6 days. In reality, many birds are likely to fly south and west where possible (Péron et al., 2011) and may be able to find unfrozen ground to feed. However, there is currently no alert within the British cold-weather shooting policy for conditions leading to frozen ground inland. Indeed, there is no common approach between countries within the wintering range to cold-weather shooting restrictions. We suggest that shooters across Europe should adopt a more cautious approach to shooting woodcock in cold weather and should stop after 4 days of frozen conditions and allow the birds at least 7 days to recover after the end of the cold period before shooting recommences. Another simple guideline for shooters would be to stop shooting woodcock when woodcock weights are below 270 g. In practice, shooting in the United Kingdom is likely to be restricted more frequently than elsewhere in Europe, but this change would not result in many more days when shooting is not permitted than under the current UK cold-weather suspension system and would afford woodcock better protection.

4.1 | Management and policy implications

(i) In the event of cold spells anywhere in Europe, woodcock shooting at a regional level should be restricted before the end of the fasting endurance period. (ii) We suggest a common shooting restraint policy, such that an alert to stop shooting woodcock is issued after 4 days of permanently frozen ground at inland sites. This should ensure the survival of around 80% of birds during frozen conditions. (iii) A "Protection Order" following a thaw, as follows the current UK statutory suspension, is important and should last at least 7 days. (iv) Policy makers should consider a system for halting woodcock shooting in any winter if there are more than two cold spells.

ACKNOWLEDGEMENTS

We thank Hugo Straker, David Clark and all hunters who collected birds, and Castle Hill and Rotherfield Park estates for hosting our woodcock ringing. Alex Fall, Joel Brittain, Arturo Oliver, José Moreno and Alice Deacon assisted with dissections. We thank Chris Heward for help with age determination and artwork, Daniel Upton and Tom Porteus for automating data analysis and Yves Ferrand for his suggestions. Mathieu Boos provided crucial advice and guidance on the use of allometric equations. Nicholas Aebischer, Gavin Siriwardena and two anonymous referees helped improve earlier drafts. The study was funded by the Game & Wildlife Conservation Trust.

AUTHORS' CONTRIBUTIONS

A.H. conceived the study and methodology; C.S. conducted dissections; A.H. and O.W. conducted woodcock ringing; A.H. and C.S. analysed the data and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.n3k9f (Sánchez-García, Williams, & Hoodless, 2018).

ORCID

Carlos Sánchez-García http://orcid.org/0000-0002-0693-6411

REFERENCES

Agencia Estatal Boletín Oficial del Estado. (2015). *Código de Caza*. https://boe.es/legislacion/codigos/codigo.php?id=095_Codigo_de_Caza&modo=1 (Accessed 13 November 16)

Aradis, A., Landucci, G., Tagliavia, M., & Bultrini, M. (2015). Sex determination of Eurasian Woodcock *Scolopax rusticola*: A molecular and morphological approach. *Avocetta*, *39*, 83–89.

Bednekoff, P. A., & Houston, A. I. (1994). Optimizing fat reserves over the entire winter: A dynamic model. *Oikos*, *71*, 408–415. https://doi.org/10.2307/3545828

Birdlife International. (2017). *Scolopax rusticola*, Eurasian woodcock. Retrieved from http://datazone.birdlife.org/species/factsheet/22693052 (Accessed 1 February 17)

Boos, M. (2000). *Modifications des réserves énergétiques corporelles du canard colvert (Anas platyrhynchos) et de la bécasse des bois (Scolopax rusticola) au cours de leur hivernage: Aspects fonctionnels liés à la biologie de ces espèces et aux conditions du milieu*. France: University of Strasbourg.

Boos, M., Boidot, J. P., & Robin, J. P. (2005). Body condition in the Eurasian Woodcock wintering in the west of France: Practical study for wildlife management during cold spells. *Wildlife Biology in Practice*, *1*, 15–23.

Davidson, N. C., & Clark, N. A. (1985). The effects of severe weather in January and February 1985 on waders in Britain. *Wader Study Group Bulletin*, *44*, 10–16.

Davidson, N. C., & Evans, P. R. (1982). Mortality of Redshanks and Oystercatchers from starvation during severe weather. *Bird Study*, *29*, 183–188. https://doi.org/10.1080/00063658209476755

Duriez, O., Eraud, C., Barbraud, C., & Ferrand, Y. (2005). Factors affecting population dynamics of Eurasian woodcocks wintering in France: Assessing the efficiency of a hunting-free reserve. *Biological Conservation*, *122*, 89–97. https://doi.org/10.1016/j.biocon.2004.07.002

Duriez, O., Fritz, H., Binet, F., Tremblay, Y., & Ferrand, Y. (2005). Individual activity rates in wintering Eurasian woodcocks: Starvation versus predation risk trade-off? *Animal Behaviour*, *69*, 39–49. https://doi.org/10.1016/j.anbehav.2004.04.009

Eaton, M., Aebischer, N. J., Brown, A. F., Hearn, R. D., Lock, L., Musgrove, A. J., … Gregory, R. D. (2015). The population status of birds in the United Kingdom. *British Birds*, *108*, 708–746.

Ellis, M. B. (2012). Management of waterfowl shooting during periods of severe weather in the UK. *Animal Biodiversity and Conservation*, *35*, 171–174.

Estoppey, F. (2001). Demographics of a breeding population of Eurasian Woodcock *Scolopax rusticola* in western Switzerland from 1989 to 2000. *Nos Oiseaux*, *48*, 105–112.

Ferrand, Y., Aubry, P., Landry, P., & Priol, P. (2013). Responses of Eurasian woodcock *Scolopax rusticola* to simulated hunting disturbance. *Wildlife Biology*, *19*, 19–29. https://doi.org/10.2981/11-058

Ferrand, Y., & Gossmann, F. (2009). Ageing and sexing series 5: Ageing and sexing the Eurasian woodcock *Scolopax rusticola*. *Wader Study Group Bulletin*, *116*, 75–79.

Gosler, A. G., Greenwood, J. J. D., & Perrins, C. (1995). Predation risk and the cost of being fat. *Nature*, *377*, 621–623. https://doi.org/10.1038/377621a0

Gossmann, F., and Ferrand Y. (1998). Impact of the 1996/1997 cold spell on woodcock in France based on ring recoveries. In H. Kakchreuter, (Eds.), Proceedings of the fifth European woodcock and snipe workshop (vol. 4, pp. 37-39). Wetlands International Global series.

Gossmann, F., Ferrand, Y., Loidon, Y., & Sardet, G. (1988). Méthodes et résultats de baguages des bécasses des bois (*Scolopax rusticola*) en Bretagne. In P. Havet & G. Hirons, *(Eds.)*, *Actes du 3éme Symposium Européen sur la Bécasse et les Bécassines* (pp. 34–41). Paris, France.

Granval, P. (1987). Régime alimentaire diurne de la Bécasse des Bois (*Scolopax rusticola*) en hivernage: approche quantitative. *Gibier Faune Sauvage*, *4*, 125–147.

Guzmán, J. L., & Arroyo, B. (2015). Predicting winter abundance of woodcock *Scolopax rusticola* using weather data: Implications for hunting management. *European Journal of Wildlife Research*, *61*, 467–474. https://doi.org/10.1007/s10344-015-0918-4

Heward, C. J., Hoodless, A. N., Conway, G. J., Aebischer, N. J., Gillings, S., & Fuller, R. J. (2015). Current status and recent trend of the Eurasian Woodcock *Scolopax rusticola* as a breeding bird in Britain. *Bird Study*, *62*, 535–551. https://doi.org/10.1080/00063657.2015.1092497

Hoodless, A. N. (1995). Studies of West Paleartic birds. 195. Eurasian Woodcock Scolopax rusticola. *British Birds*, *88*, 578–592.

Hoodless, A. N., & Coulson, J. C. (1994). Survival rates and movements of British and Continental Woodcock *Scolopax rusticola* in the British Isles. *Bird Study*, *41*, 48–60. https://doi.org/10.1080/00063659409477197

Hoodless, A. N., & Hirons, G. J. M. (2007). Habitat selection and foraging behaviour of breeding Eurasian Woodcock *Scolopax rusticola*: A comparison. *Ibis*, *149*, 234–249. https://doi.org/10.1111/j.1474-919X.2007.00725.x

Hoodless, A. N., Lang, D., Aebischer, N. J., Fuller, R. J., & Ewald, A. (2009). Densities and population estimates of breeding Eurasian Woodcock *Scolopax rusticola* in Britain in 2003. *Bird Study*, *56*, 15–25. https://doi.org/10.1080/00063650802674768

Hoodless, A. N., Powell, A., Ferrand, Y., Gosler, A., Fox, J., Newton, J., & Williams, O. (2013). Application of new technologies to the study of Eurasian Woodcock migration. In Y. Ferrand (Ed.), *Seventh European woodcock and snipe workshop* (pp. 7–18). Paris, France: Office National de la Chasse et de la Faune Sauvage.

Jenni, L., & Jenni-Eiermann, S. (1998). Fuel supply and metabolic constraints in migrating birds. *Journal of Avian Biology*, *29*, 521–528. https://doi.org/10.2307/3677171

Lima, S. L. (1986). Predation risk and unpredictable feeding conditions: Determinants of body mass in birds. *Ecology*, *67*, 377–385. https://doi.org/10.2307/1938580

Lormée, H., Ferrand, Y., Bastat, C., Coreau, D., Gossmann, F., Trolliet, B., … Boutin, J. M. (2013). Effects of the February 2012 cold spell on terrestrial birds wintering in France. *Ringing & Migration*, *28*, 85–97. https://doi.org/10.1080/03078698.2013.869899

Lutz, M., & Jensen, F. (2006). European Union Management Plan for Woodcock Scolopax Rusticola. 2007–2009. http://www.woodcockireland.com/mngt_plan.doc (Accessed 13 November 2016)

MacDonald, D. W. (1983). Predation on earthworms by terrestrial predators. In J. E. Satchell (Ed.), *Earthworm ecology: From Darwin to Vermiculture* (pp. 393–414). London, UK: Chapman and Hall Ltd. https://doi.org/10.1007/978-94-009-5965-1

MEDDTL (Ministère de l'Environnement, de l'Energie et de la Mer). (2010). http://www.bulletin-officiel.developpement-durable.gouv.fr/fiches/BO201023/met (Accessed 3 May 2015)

Mitchell, P. I., Scott, I., & Evans, P. R. (2000). Vulnerability to severe weather and regulation of body mass of Icelandic and British Redshank *Tringa totanus*. *Journal of Avian Biology*, *31*, 511–521. https://doi.org/10.1034/j.1600-048X.2000.1310411.x

Newton, I. (1998). *Population limitation in birds*. London, UK: Academic Press Limited.

Péron, G., Ferrand, Y., Choquet, R., Pradel, R., Gossmann, F., Bastat, C., … Gimenez, O. (2012). Spatial heterogeneity in mortality and its impact on the population dynamics of Eurasian woodcocks. *Population ecology*, *54*, 305–312. https://doi.org/10.1007/s10144-012-0309-6

Péron, G., Ferrand, Y., Gossmann, F., Bastat, C., Guénézan, M., & Gimenez, O. (2011). Escape migration decisions in Eurasian Woodcocks: Insights from survival analyses using large-scale recovery data. *Behavioral Ecology and Sociobiology*, *65*, 1949–1955. https://doi.org/10.1007/s00265-011-1204-4

Powell, A. (2012). *Origins and non-breeding ecology of Eurasian woodcock*. Oxford, UK: University of Oxford.

Prior, J., & Kendon, M. (2011). The disruptive snowfalls and very low temperatures of late 2010. *Weather*, *66*, 315–321. https://doi.org/10.1002/wea.874

Sánchez-García, C., Williams, O., & Hoodless, A. (2018). Data from: Regulation of body reserves in a hunted wader: Implications for cold-weather shooting restrictions. *Dryad Digital Repository*, https://doi.org/doi:10.5061/dryad.n3k9f

Soriano-Redondo, A., Bearhop, S., Cleasby, I. R., Lock, L., Votier, S. C., & Hilton, G. M. (2016). Ecological responses to extreme flooding events: A case study with a reintroduced bird. *Scientific Reports*, *6*, 28595. https://doi.org/10.1038/srep28595

Stroud, D. A., Harradine, J. P., Shedden, C., Hughes, J., Williams, G., Clark, J. A., & Clark, N. A. (2006). Reducing waterbird mortality in severe cold weather: 25 years of statutory suspensions in Britain. In G. C. Boere, C. A. Galbraith, & D. A. Stroud (Eds.), *Waterbirds around the world* (pp. 784–790). Edinburgh, UK: The Stationery Office.

Tavecchia, G., Pradel, R., Gossman, F., Bastat, C., Ferrand, Y., & Lebreton, J. D. (2002). Temporal variation in annual survival probability of the Eurasian woodcock *Scolopax rusticola* wintering in France. *Wildlife Biology*, *8*, 21–30.

Thorup, O. (2006). *Breeding waders in Europe 2000*. Thetford, UK: International Wader Study Group.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Sánchez-García C, Williams O, Hoodless A. Regulation of body reserves in a hunted wader: Implications for cold-weather shooting restrictions. *J Appl Ecol*. 2018;55:2274–2284. https://doi.org/10.1111/1365-2664.13128