diversity

Article

Substantial Variation in Prospecting Behaviour of Young Golden Eagles *Aquila chrysaetos* Defies Expectations from Potential Predictors

Alan H. Fielding [1], David Anderson [2], Stuart Benn [3], Robin Reid [4], Ruth Tingay [5], Ewan D. Weston [1] and D. Philip Whitfield [1,*]

[1] Natural Research Ltd., Brathens, Aberdeenshire AB31 4BY, UK; a.h.fielding@gmail.com (A.H.F.); ewan_weston@hotmail.com (E.D.W.)
[2] Dave Anderson Ecology Ltd., Callander FK17 8EU, UK; dikanderson@googlemail.com
[3] RSPB Scotland, Inverness IV2 3BW, UK; stuart@polarfox.myzen.co.uk
[4] Independent Researcher, Isle of Harris HS3 3EZ, UK; vikingrobin@hotmail.com
[5] Wild Justice, 9 Lawson Street, Raunds, Northants NN9 6NG, UK
* Correspondence: phil.whitfield@natural-research.org

Abstract: Natal dispersal of large raptors is poorly understood, despite being a crucial transitional life-cycle phase affecting gene flow and population dynamics. A research-gap rarely examined concerns how young dispersing raptors strategize movements towards first settlement on a prospective breeding territory. First territory settlement is a critical decision for a lifetime and can take several years. With such importance, large raptors should theoretically devote considerable effort to acquire accurate information during prospection. Nevertheless, when discovery of territorial opportunities may be difficult, but easier in vacant territories, we posit two extremes in strategizing prospection behaviours: (1) "Quick, grab it when available with limited reconnaissance", as opposed to (2) "Slow, waiting game with frequent reconnaissance". We analysed pre-settlement data from 37 GPS-tagged nestling golden eagles, later recorded as having settled on their first territory. The number of eagles' unique daily visits to their later settled territories was a measure of prospection intensity. We documented substantial variation in prior visits, between less than 10 to several hundred. Analyses considered several potential predictors. We expected a positive association between number of prospecting visits and natal dispersal duration, since with more time to gather information there should be more visits. We also expected fewer prospecting visits in prior vacant territories. Neither of these expectations were supported. There was a non-significant tendency for more prospection visits by males. Our study provides novel information on a seldom-studied behaviour in a large raptor. It illustrates substantial variation in prospecting behaviour, but expectations of potential drivers behind this variation were not confirmed, urging further study.

Keywords: reconnaissance behaviour; natal dispersal; juvenile dispersal; transience phase; raptor; population ecology; GPS-telemetry

check for updates

Citation: Fielding, A.H.; Anderson, D.; Benn, S.; Reid, R.; Tingay, R.; Weston, E.D.; Whitfield, D.P. Substantial Variation in Prospecting Behaviour of Young Golden Eagles *Aquila chrysaetos* Defies Expectations from Potential Predictors. *Diversity* **2023**, *15*, 506. https://doi.org/10.3390/d15040506

Academic Editors: Michael Wink, Vladimir D. Dobrev, Dobromir D. Dobrev and Dimitar A. Demerdzhiev

Received: 21 February 2023
Revised: 24 March 2023
Accepted: 27 March 2023
Published: 1 April 2023

1. Introduction

Much of the behaviour of large raptors during natal dispersal [1,2], often termed juvenile dispersal [3–7], is poorly known [8]. This is the phase between birds departing from their natal range (at the end of post-fledging dependence phase: PFDP [7,9]) and settlement on a prospective breeding territory [10]. A particular research-gap in this critical phase, otherwise termed as transience [7,11–14], involves how dispersing birds prospect or may strategize their first settlement on a breeding territory [14,15].

First territory settlement in large raptors is important because it is substantially a decision for a lifetime via territory quality, available partner, and hence reproductive resources. After initial settlement, further movements (via breeding dispersal: [1]) appear uncommon in most species [10,16,17]. While large raptors can take several years during natal dispersal to decide on or find a prospective breeding territory in which to settle, natal dispersal is variable in duration [10].

Young large raptors face challenges in prospecting and finding any available territorial opportunity which may lead to reproduction. Life history traits, notably high longevity, and low density as top predators [16], can produce a conspecific landscape into which youngsters try to establish themselves as a reproductive entity that is typically thinly spread, usually filled with defensive occupants, and with few territorial openings for easy entry [10]. Those openings are also sought by other prospecting youngsters. Existing territorial birds, by regularly visiting neighbouring territories, likely scoping an advantageous movement, are an additional competitive element faced by dispersing youngsters [10,18]. Such opportunities may be so low in high density populations that older adults may still be 'floaters' seeking settlement where reproduction is possible [19–21].

From research on other species, prospecting future breeding opportunities may be arguably easier in species which are cavity nesting or clumped in distribution, such as colonial seabirds [15,22–25], even though prospection studies often involve breeding dispersal [26,27].

There are few studies of large raptors. Prospecting behaviour in young eagle owls *Bubo bubo* was uncommon [28]. Dispersing owls occupied long-term 'temporary settlement areas' (TSAs) close to breeding ranges with minimal prospecting, even though a few young owls rapidly occupied a breeding territory [28]. While revelatory, these features may be unusual. In other large raptors, such as the golden eagle *Aquila chrysaetos*, superficially there are far greater movements during natal dispersal which involve potential prospection, with shorter occupancy of TSAs [5,6,10,14,29].

Information gathering during prospection can be costly in time and energy [8,22], and may include death according to golden eagle studies [29–31]. Theory expects that, given the settlement decision's importance, birds should devote considerable effort to acquiring accurate information about potential locations before finally selecting a breeding site [23]. At some point, however, potential breeders must gain information regarding prospective breeding sites without the costs of gathering the information outweighing the benefits [32].

Scottish golden eagles settled when younger in prior vacant territories than in prior occupied territories, so time taken to settle was a function of the competitive environment [10]. This environment may also be relevant to prospecting behaviours under a cost-benefit evaluation [32]. Birds may nevertheless be constrained spatially in their information gathering movements by an innate natal dispersal distance (NDD: [1]) exerting a philopatric pull towards natal sites, potentially affecting prospecting movement behaviours. This philopatric pull is expected to be greater in males than females [1,2,33,34] and was confirmed in our study population [35].

Within this NDD constraint, and with a Scottish territorial landscape which can vary geographically between several vacant openings but with a higher density of occupied territories elsewhere [10,29], two respective extremes in strategizing prospection of territory availability may be: (1) "Quick, grab it when available with limited reconnaissance", as opposed to (2) "Slow, waiting game with frequent reconnaissance".

In simple cost-benefit analysis, tactic 1 avoids much prospecting cost but may not benefit subsequently from reconnoitering the best opportunity available within a limited time span. Tactic 2 encompasses the opposite strategy. These two extremes may be relevant to prospecting behaviours because in our study system eagles settled on a prospective breeding territory when younger if it was vacant. They took longer to settle on a territory which was occupied [10]. These results came from satellite telemetry research. Satellite telemetry provides novel research opportunities in avian ecology and behaviour [36], including tracking prospecting movements [15], although in large raptors it has been seldom utilised [14].

Using records of golden eagles GPS-tagged as nestlings which later settled on a territory [10], our objectives were first to describe the number of unique daily visits made during natal dispersal to the later settled territory, as a measure of prospection intensity. Under a second objective, this variable was set analytically against several potential predictors which we expected could be influential in affecting our prospection metric.

2. Methods

2.1. Study Area and Species

Scotland covers c. 80,000 km^2 on the northwestern limit of Europe and hosts around 500 territorial golden eagle pairs occupying Scotland's uplands [37], which are also used by non-territorial birds [29,38–40]. These uplands vary in geology, vegetation, topography and climatic influences.

Climatically, situated on the northeastern edge of the Atlantic Ocean, the west of Scotland being subjected more to the Atlantic Drift is wetter and windier with more equitable seasonal changes in weather, and is hence more oceanic. The east is drier with greater seasonal change in weather and is more continental [38,41]. The contrasting oceanic/continental influences tend to produce upland vegetations which are found only at higher altitude in the east but which may occur at sea level in the west. The preferred open habitats are vegetated by dry or wet heathland and peatland dominated by heather *Calluna vulgaris* and relatives in the east, with graminoids, sedges and deeper peatland more common in the west [38,41].

There is a broad west/east divide on the strong influence of illegal persecution of golden eagles. In the east, driven shoots of red grouse (*Lagopus lagopus scotica*) are practiced and require management for extremely high densities of grouse coveys [38,42–46]. To maintain such high densities, some land managers illegally kill predators of grouse such as golden eagles. Illegal persecution of golden eagles has been evident for several decades. These illegal activities substantially contribute to a national environment of numerous vacant eagle territories and a relatively low density in the east, compared to higher densities further west [29,37,38,41–46]. Such eastern areas can be attractive to eagles, but as they can be lethal, this provides a classic example of an "ecological black hole" due to anthropogenic activities [38,43,44].

The west/east influences are also reflected in golden eagles' diet in being more restricted to red grouse and mountain hares *Lepus timidus* in the east [41,47]. Despite large numbers of hares being culled on some intensively managed grouse moors [48] the abundance of red grouse and hares in the east is often associated with higher breeding productivity there, from the fewer territories which prevail—even if only sometimes temporarily [38,41–47]. In the oceanic west, climatic influences may explain much productivity variation [49], although a low dietary diversity ('specialization') was not associated with higher productivity [50].

Golden eagles in Scotland do not use lowland habitats [39,40]. They do use low altitude habitats in the western Highlands and Islands, but given the strong oceanic influences here, the "uplands" can often descend to sea-level. Topographic measures, as a surrogate for availability of orographic/declivity, winds and aerial habitat facilitating movement involving combined measures of altitude, slope and distance from ridge, are powerful predictors of golden eagle activity [39].

2.2. GPS Satellite Tagging

Tagging methods for Scottish golden eagles have been repeatedly described [7,9,29,39,40,51]. Nestlings were tagged when 50–70 days old [52,53] with transmitter weights and harnesses less than the 3% lower recommended maximum of body weight [54] (see also [55,56]). Using 13 mm tubular Teflon ribbon (Bally Ribbon Mills, Bally, PA, USA) sewed with cotton or linen thread, all birds were fitted with a thoracic X strap harness [57,58], otherwise called a "crossover wing harness" [59] or a "Garcelon-type harness" [60]. This method, and others associated with tagging, were followed [58,61]. This harness design did not affect several raptors on survival or physical injuries, including golden eagle [60]. Tagging of Scottish eagles had no apparent adverse effects under these metrics and others, including breeding productivity [29].

Several solar-charged transmitter models were deployed [9,29]. Almost all deployed tags in the present study were manufactured by MTI (Microwave Telemetry Inc., Columbia, MD, USA), and their specifications and transmission outputs are described elsewhere [7,9,10,29,39,40,51].

2.3. Estimating Variables and Statistical Analyses

Territory settlement was determined algorithmically, involving spatial and temporal evaluations accounting for potentially confounding TSA use and exploratory movements by settled territorial birds [10]. The same telemetry data were used to estimate the territory's 95% percent volume contour (PVC) using the kernel density estimator in the adehabitatHR package in R [62]. We refer to this subsequently as the range.

We recorded the number of unique days when the range was visited prior to settlement (after the post-fledging dependence period: PFDP [7,9]) using available daily points ascertained by the polygon tool of QGIS 3.26. This was taken as our measure of prospection intensity, in description and as the dependent variable in analyses. We did not use the number of records in the range as this metric would be more affected by the state of a tag's battery and its solar recharge, which can decline in winter and in darkness [63]. Nocturnal records were excluded using the R suncalc package (v 0.5.0) [64].

We utilized five potential predictors (explanatory variables) in our analyses:

1. The duration of natal dispersal taken as dates between when an eagle dispersed (after PFDP: [7]) and when it settled on a territory [10]. This was expected to be influential, since with longer natal dispersal, opportunities for more prospection visits were greater.
2. The prior status of the settled territory: occupied or vacant [10]. Under our premise on 'quick' or 'slow' reconnaissance (Introduction), the ease of prospection and settlement should be greater in vacant territories—towards the 'quick' premise.
3. The duration to first date after dispersing (i.e., post-PFDP) when an eagle first visited its later settled territory. We included this variable under the premise that early experience of the settled territory may have had an influence on how quickly later settlement occurred.
4. The duration of PFDP. The beginning of PFDP for birds tagged as nestlings was taken as a generic fledging date of 1 August, to first date of dispersal on duration [7,9]. These measures gave the start and end dates of the metric. This metric was included as a potential predictor because PFDP is highly variable [7,9] and if birds spend more time in their natal territory, then this could have consequences for their later prospection efforts.
5. Sex. Differences between sexes surrounding natal dispersal are several [1,2,7,9,10,33–35].

Using R (v 4.2.3), we computed single predictor general linear models (GLMs) with Gaussian error distribution. Predictor significance was obtained using the R summary command. Given that there were five potential predictors, there were many potential multi-predictor models. We used the dredge function from the R MuMIn package (v 1.47.1) for multi-model inference and used AIC to rank the models. We selected the model with the lowest AIC as the best model but we acknowledged a warning [65] about selecting a spurious best model, and therefore we included parsimony as an important criterion.

3. Results

Our study involved 37 tagged eagles (Table 1). Summary descriptive statistics showed that there was a wide variation in the number of days when young eagles visited their future territorial range prior to settlement, from one to 493 (minimum and maximum values) (Table 2).

We fitted GLM models, estimated using maximum likelihood, using prior unique daily visits to the future range as the dependent and the five potential predictors (Methods) as prospective explanatories. None of the predictors was significant when used in isolation (Table 3). We also fitted a full model but its explanatory power to predict the number of visits to the future range was weak ($R^2 = 0.09$). The full model's intercept, corresponding to sex = F, prior status = occupied, days to first visit = 0, natal dispersal duration = 0 and PFDP duration = 0, was at 118.41 (95% CI [−71.27, 308.09], t (df = 31) = 1.22, $p = 0.221$).

Table 1. Raw data used in analyses. Tag = Tag ID, Sex (M = male, F = female), Dispersal = date of dispersal (end of PFDP: d/m/y), PFDP = duration of PFDP (d), 1st visit = date of first visit to future range, Day 1 = 1st visit to future range (d) where 0 = start of dispersal, Visits = number of unique dates (d) on which the settled range was visited, Settled = date the bird settled (d/m/y), Duration = natal dispersal duration (d) (number of days to settlement from the start of dispersal, day 0), NDD = Distance from natal site to future range (km), Prior Status = status of the future range prior to settlement (O = occupied, V = vacant).

Tag	Sex	Dispersal	PFDP	1st Visit	Day 1	Visits	Settled	Duration	NDD	Prior Status
100	M	04/02/15	173	14/03/15	38	187	22/03/19	1507	60	O
102	F	01/11/08	78	09/11/08	8	7	07/02/12	1193	58.6	O
334	M	09/12/16	116	12/04/17	124	64	25/09/18	655	26.9	V
582	F	07/11/16	84	10/04/17	154	67	06/03/21	1580	60	O
584	M	12/04/16	241	13/04/17	366	283	16/10/21	2013	18	V
660	M	01/03/18	198	18/04/18	48	70	06/01/19	311	13.6	V
809	F	22/09/16	38	04/04/17	194	32	24/05/20	1340	63	O
815	F	04/03/09	201	05/10/11	945	1	01/03/14	1823	25	O
928	M	03/02/18	172	25/02/18	22	31	29/04/21	1181	36	O
932	M	21/03/18	218	02/08/19	499	48	07/10/19	565	43.1	V
933	F	19/09/19	32	14/09/20	361	9	20/04/22	944	50.8	V
1025	M	20/01/19	158	14/03/19	83	40	10/09/21	964	35	V
1026	M	11/03/19	208	20/01/20	315	38	08/12/21	1003	52	V
1030	F	28/10/18	74	09/04/19	163	73	19/04/21	904	68	V
1031	M	01/04/19	229	02/04/19	1	461	06/09/20	524	66	V
1074	F	31/10/19	77	02/03/20	123	315	07/02/21	465	83	V
1094	M	06/12/19	113	26/04/20	142	226	17/12/21	742	81.9	V
1096	F	30/10/19	76	21/11/19	22	402	19/05/21	567	12	O
1097	M	30/10/19	76	25/04/22	908	493	29/08/22	1034	33.1	O
21197	F	28/12/10	135	02/05/11	125	7	23/01/13	757	78	O
51888	M	03/03/15	200	05/09/15	186	31	04/02/18	1069	27	O
57109	M	28/09/10	44	08/02/11	133	357	20/02/15	1606	33	O
57115	M	17/10/10	63	27/03/11	161	42	23/10/11	371	30	V
84135	F	17/10/10	63	28/06/11	254	54	15/12/11	424	82	V
89251	F	05/02/12	174	27/06/13	508	13	17/12/14	1046	65	O
89279	F	17/12/11	124	11/02/12	56	114	16/02/16	1522	38	O
120196	M	04/11/12	81	26/03/14	507	8	10/04/15	887	29	O
129005	M	06/11/13	83	08/11/13	2	20	21/01/16	806	26	V
129006	M	05/10/13	51	26/10/13	21	110	15/01/19	1928	26	O
129008	F	31/10/14	77	02/06/15	214	26	12/11/16	743	32	V
129012	M	05/12/13	112	11/01/14	37	301	07/04/15	488	13	V
148632	F	28/11/15	105	27/03/16	120	64	14/02/17	444	40	V
148635	F	25/10/15	71	04/03/17	496	2	10/03/17	502	87	V
148639	F	11/02/16	180	20/04/16	69	65	02/05/17	446	56	V
148640	M	05/02/16	174	21/02/16	16	100	20/02/17	381	42	V
286611	F	10/11/07	87	13/03/09	489	2	05/04/09	512	67	V
656352	M	22/03/09	219	14/04/09	23	65	31/03/12	1105	29	O

Table 2. Descriptive statistics for the explanatory variable (home range visits: number of unique days), and predictive variables: natal dispersal duration, first visit to the future range and duration of PFDP. These are cast according to sex (M = male F = female) and the status of the future range prior to settlement (occupied or vacant). LCL = 2.5% quantile, UCL = 97.5% quantile.

Variable	Sex	Prior Status	Min	LCL	Mean	Median	UCL	Max	sd
Home range visits (d)	F	occupied	1	2	80	23	352	402	136
	F	vacant	2	2	68	54	267	315	97
	M	occupied	8	12	160	88	469	493	177
	M	vacant	20	25	141	67	417	461	142
Natal dispersal duration (d)	F	occupied	567	600	1228	1266	1780	1823	426
	F	vacant	424	428	598	502	936	944	208
	M	occupied	887	913	1290	1143	1872	1928	354
	M	vacant	311	328	735	610	1735	2013	461
First visit to future range (d)	F	occupied	8	11	252	140	869	945	322
	F	vacant	69	79	254	214	495	496	160
	M	occupied	21	21	230	86	838	908	319
	M	vacant	1	1	150	104	462	499	161
Duration of PFDP (d)	F	occupied	38	45	114	104	196	201	55
	F	vacant	32	38	85	77	165	180	41
	M	occupied	44	45	127	126	216	219	71
	M	vacant	63	69	159	166	238	241	61

Table 3. Results of individual Gaussian GLMs estimated by maximum likelihood using number of visits to the future range as the response (dependent) variable. Prospective explanatory predictor variables involved sex (male or female), duration of natal dispersal, prior occupancy status (occupied or vacant), days to first visit after dispersing and duration of PFDP.

Predictor	Beta	95% CI: Lower, Upper	*t* (df)	Standard Beta (95% CI)	*p*
Sex (corresponding to F)					
Sex (M)	75.04	−12.84, 162.93	1.67 (35)	0.54 (−0.09, 1.17)	0.094
Natal dispersal duration (corresponding to zero)					
Natal dispersal duration (d)	0.0	0.08, 0.11	0.29 (35)	0.05 (−0.28, 0.38)	0.775
Prior occupancy status (corresponding to vacant)					
Prior occupancy status (occupied)	−10.65	−102.45, 81.16	−0.23 (35)	−0.08 (−0.74, 0.58)	0.820
First day to range visit (corresponding to zero)					
First visit to future range (d)	0.00	−0.09, 0.11	0.16 (35)	0.03 (−0.30, 0.36)	0.870
Duration of PFDP (corresponding to zero)					
Duration of PFDP (d)	−0.73	−0.73, 0.75	0.03 (35)	0.01 (−0.33, 0.34)	0.976

There were no significant results indicating any potential predictor variable's influence (Table 3). An influence of sex was suggested (Table 3: $p = 0.094$) such that males tended to make more prospection visits to the future range and had a greater spread of prior visitation efforts than females (Figure 1).

Multi-model inference using the dredge function identified the highest ranked model, out of 16, as one with sex as the only predictor approaching possible influence. Sex was insignificant in this single predictor model, however, and the adjusted R^2 (0.032) was weak. This highest ranked model had an AIC of 535.8, while the second highest ranked model was the null model with an AIC of 536.2 (delta AIC = 0.42). Using parsimony, and the absence of a significant predictor in the highest ranked model, the null model was selected as the 'best' model. Hence, the absence of significant predictors, out of those tested, was confirmed.

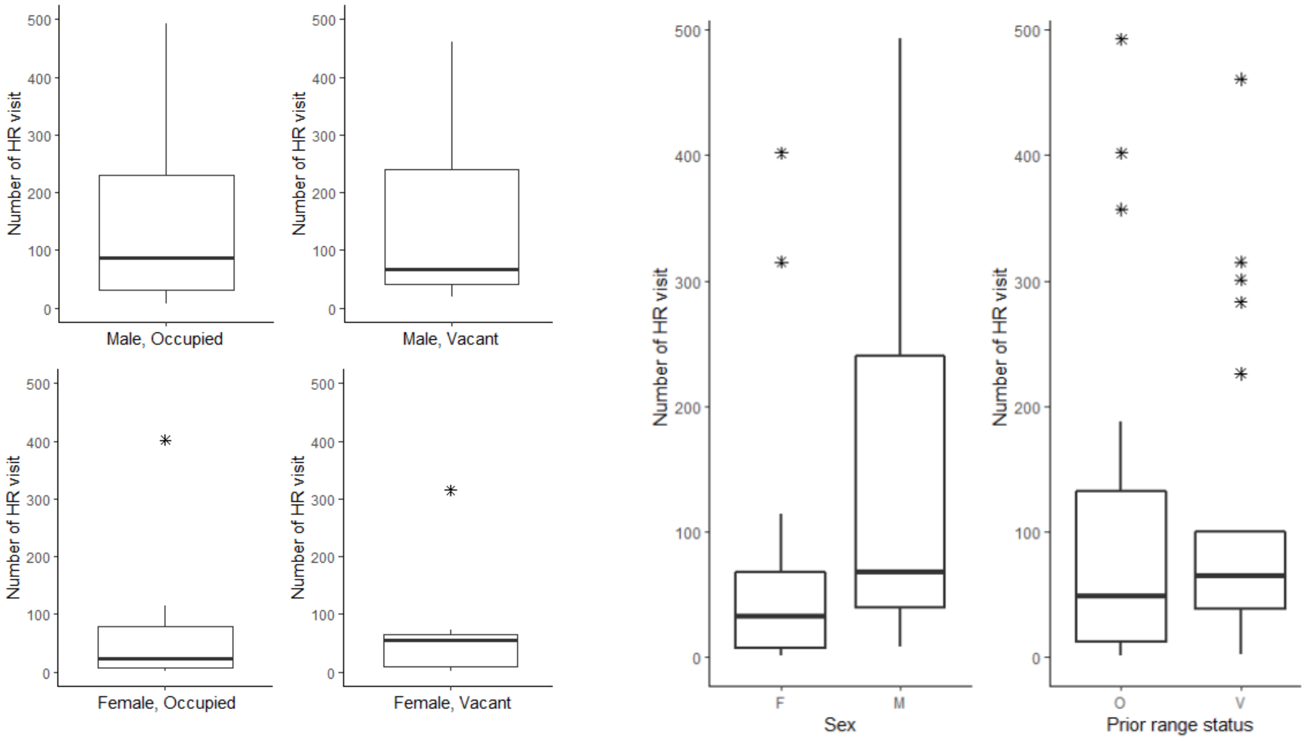

Figure 1. Illustrations of some results from analyses, with number of daily prior visits to the home range as the dependent variable (y axes). Presentations are box and whisker plots according to selected independent predictor variables (x axes). Solid black horizontal lines show medians, and box limits correspond to the first and third quartiles (25 and 75 percentiles). Whiskers (vertical lines) show values extending 1.5 times away from this inter-quartile range, and asterisks show values which were greater. The upper panels show results for sex and prior range status. With the suggestion of some influence of sex (upper left graphic), the middle panels show results for males according to prior range status (vacant or occupied), with corresponding results for females in the bottom panels.

4. Discussion

Golden eagles showed a wide range of prospection behaviours in how often the future settled territory was visited during natal dispersal, from a handful of visits to hundreds. This is a novel result in a field seldom considered previously in large raptors [14]. It is different to eagle owls in southern Spain [28].

We did not find any relationships with the large variation in our prospection metric. Two reasonable expectations were not supported as influential. Duration of natal dispersal (allowing more time for prospection) was not related. Prior occupancy status (if vacant then ease of settlement should produce fewer visits) was also not related, even though eagles settle when younger in vacant territories [10]. Such youthful settlement would expect fewer prospection visits but was not supported.

We posited two extremities for eagles' strategizing prospection behaviours: (1) "Quick, grab it when available with limited reconnaissance", as opposed to (2) "Slow, waiting game with frequent reconnaissance". Broadly, this was recorded. Tactic 1 should be more likely in vacant territories, however, and tactic 2 should be more likely in occupied territories. In some environments, the best territories should be more in demand and thus subject to more competition with a potentially longer waiting list for occupancy of higher quality territories [66]. This would result in more time to discover a territorial opening and more visits to reconnoiter any opening in higher quality territories.

This was not our study's environment, however. Critical to our study is that it involved a territorial landscape which was heavily influenced by illegal persecution, which has created many territorial vacancies in parts of eastern regions (Methods). We did not have data to explore settlement and prior prospecting behavioural decisions against subsequent reproductive outputs from settled birds, not least as age of occupants can affect reproductive success [43], and age of settlement is also variable and often young [10]. Nonetheless, in eastern regions where fewer territories are occupied, reproductive outputs are typically higher [38,45,46]. The waiting list [66] for such high-quality territories is therefore disproportionately shortened because of illegal persecution.

Hence, eagles settle when younger on these territories [10], and counter-intuitively, through effects of persecution, higher quality (vacant) territories were consequently expected to have a shorter waiting list with less reconnaissance during prospection. This was not found, however.

We also found no evidence that the rapidity with which an eagle first visited its later territory had any relationship with how often it was visited subsequently. Nor was there any relationship between the duration of PFDP—which can be highly variable [7,9]—with the substantial variation in prospection visits to the settled territory.

There was a non-significant indication that males made more prospection visits than females. This could be explained if males were more pioneering and active in establishing a new territory, since there were numerous vacant territories in our study system ([10,29,35], present study: Table 1). The role of females would arguably be more attuned to selecting a territory and their prospective male partner, and so with slightly later settlement. In a re-introduced population of white-tailed eagles *Haliaeetus albicilla*, this sequence of events was indicated [17]; however, see [67]. An earlier analysis of golden eagles in Scotland, however, did not find earlier settlement of males, even in vacant territories [10]. Including the present study, nonetheless, there is increasing evidence of differences between males and females, at stages involving natal dispersal which are still to be explained [9,10,35].

It is inevitable that dispersing birds will have visited several occupied ranges, and it is possible that the location and number of occupied ranges visited played a role in an individual's decision to settle. However, we were unable to investigate this because we did not have contemporaneous complete records of all occupied ranges across Scotland. This is a weakness in our study which is unlikely to be overcome in any reasonably sized population of large raptors.

In conclusion, we showed that young golden eagles had marked extremes in their reconnaissance tactics, completing very few to hundreds of prospection visits. We did not discover any significant predictors behind this variation, despite reasonable expectations under several potential explanatory variables. This illustrates that for large raptors it is a research field deserving more attention, if only initially on simple descriptive estimates of prospection behaviours [14].

Author Contributions: Conceptualization, A.H.F. and D.P.W.; methodology, all authors; validation, A.H.F. and D.P.W.; formal analysis, A.H.F. and D.P.W.; investigation, all authors; data curation, A.H.F.; writing-original draft preparation, A.H.F. and D.P.W.; writing-review and editing, all authors; visualization, all authors; supervision, A.H.F. and D.P.W.; project administration, D.P.W.; funding acquisition, D.P.W., R.T., D.A. and S.B. All authors have read and agreed to the published version of the manuscript.

Funding: Funding of tags and data download costs notably came from Natural Research, the Royal Society for the Protection of Birds, Roy Dennis Wildlife Foundation, Ruth Tingay and SSE Renewables. We are grateful to Emma Ahart, Thomas Plant, Nicki Small and Jenny Chambers (SSE Renewables) and Peter Robson (Scottish Power Renewables) for gaining permission to use data and to encourage tag funding, and to Chris Donald for a few tags funded by SNH. Two tags were provided by Movetech. Manuscript production was financially supported by SSE under the research programme of the Regional Eagle Conservation Management Plan. For facilitating this continued support, we thank Nicki Small and Jenny Chambers most recently. Despite this support, SSE had no influence or commentary in the production of the manuscript. Funding for open access publication was provided by Natural Research Ltd.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Raw data are presented in Table 1. We cannot publicly or responsibly provide grid references for natal nest sites or subsequent settled territorial nest sites through prohibition under UK legislative practice.

Acknowledgments: Tagging was undertaken by David Anderson, Roy Dennis, Brian Etheridge, Justin Grant, Duncan Orr-Ewing and Ewan Weston: all were appropriately licensed under disturbance, handling, ringing and tagging licences from SNH (Scottish Natural Heritage: latterly NatureScot) and British Trust for Ornithology (BTO). We are extremely grateful for the considerable supporting fieldwork from many members of the Scottish Raptor Study Group. Staff at MTI (tag manufacture and support) and BTO (licensing) were helpful.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Greenwood, P.J. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **1980**, *28*, 1140–1162. [CrossRef]
2. Greenwood, P.J.; Harvey, P.H. The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.* **1982**, *13*, 83–88. [CrossRef]
3. Ferrer, M. Ontogeny of dispersal distances in young Spanish imperial eagles. *Behav. Ecol. Sociobiol.* **1993**, *32*, 259–263. [CrossRef]
4. Ferrer, M. Juvenile dispersal behavior and natal philopatry of a long-lived raptor, the Spanish Imperial Eagle *Aquila adalberti*. *Ibis* **1993**, *135*, 132–138. [CrossRef]
5. Whitfield, D.P.; Duffy, K.; McLeod, D.R.A.; Evans, R.J.; MacLennan, A.M.; Reid, R.; Sexton, D.; Wilson, J.D.; Douse, A. Juvenile dispersal of White-tailed Eagles in western Scotland. *J. Raptor Res.* **2009**, *43*, 110–120. [CrossRef]
6. Weston, E.D. Juvenile Dispersal Behaviour in the Golden Eagle (*Aquila chrysaetos*). Ph.D. Thesis, University of Aberdeen, Aberdeen, UK, 2014.
7. Weston, E.D.; Whitfield, D.P.; Travis, J.M.T.; Lambin, X. When do young birds disperse? Tests from studies of golden eagles in Scotland. *BMC Ecol.* **2013**, *13*, 42. [CrossRef]
8. Clobert, J.; Le Galliard, J.F.; Cote, J.; Meylan, S.; Massot, M. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett.* **2009**, *12*, 197–209. [CrossRef]
9. Weston, E.D.; Whitfield, D.P.; Travis, J.M.T.; Lambin, X. The contribution of flight capability to the post-fledging dependence period of golden eagles. *J. Avian Biol.* **2018**, *49*, e01265. [CrossRef]
10. Whitfield, D.P.; Fielding, A.H.; Anderson, D.; Benn, S.; Dennis, R.; Grant, J.; Weston, E.D. Age of first territory settlement of Golden Eagles *Aquila chrysaetos* in a variable competitive landscape. *Front. Ecol. Evol.* **2022**, *10*, 743598. [CrossRef]
11. Stenseth, N.C.; Lidicker, W.Z. The study of dispersal: A conceptual guide. In *Animal Dispersal: Small Mammals as a Model*; Stenseth, N.C., Lidicker, W.Z., Jr., Eds.; Chapman and Hall: London, UK, 1992; pp. 5–20.
12. Delgado, M.M.; Penteriani, V. Behavioral states help translate dispersal movements into spatial distribution patterns of floaters. *Am. Nat.* **2008**, *172*, 475–485. [CrossRef]
13. Delgado, M.M.; Penteriani, V.; Nams, V.O.; Campioni, L. Changes of movement patterns from early dispersal to settlement. *Behav. Ecol. Sociobiol.* **2009**, *64*, 35–43. [CrossRef]
14. Poessel, S.A.; Woodbridge, B.; Smith, B.W.; Murphy, R.K.; Bedrosian, B.E.; Bell, D.A.; Bittner, D.; Bloom, P.H.; Crandall, R.H.; Domenech, R.; et al. Interpreting long-distance movements of non-migratory golden eagles: Prospecting and nomadism? *Ecosphere* **2022**, *13*, e4072. [CrossRef]
15. Ponchon, A.; Grémillet, D.; Doligez, B.; Chambert, T.; Tveraa, T.; González-Solís, J.; Boulinier, T. Tracking prospecting movements involved in breeding habitat selection: Insights, pitfalls and perspectives. *Methods Ecol. Evol.* **2013**, *4*, 143–150. [CrossRef]
16. Newton, I. *Population Ecology of Raptors*; Poyser: Berkhamstead, UK, 1979.
17. Whitfield, D.P.; Douse, A.; Evans, R.J.; Grant, J.; Love, J.; McLeod, D.R.A.; Reid, R.; Wilson, J.D. Natal and breeding dispersal in a reintroduced population of White-tailed Eagles *Haliaeetus albicilla*. *Bird Study* **2009**, *56*, 177–186. [CrossRef]
18. Watson, J.E.; Duff, A.A.; Davies, R.W. Home range and resource selection by GPS-monitored adult Golden Eagles in the Columbia plateau ecoregion: Implications for wind power development. *J. Wildl. Manag.* **2014**, *78*, 1012–1021. [CrossRef]
19. Hunt, W.G. Raptor floaters at Moffat's equilibrium. *Oikos* **1998**, *82*, 191–197. [CrossRef]
20. Penteriani, V.; Otalora, F.; Ferrer, M. Floater survival affects population persistence. The role of prey availability and environmental stochasticity. *Oikos* **2005**, *108*, 523–534. [CrossRef]
21. Sergio, F.; Tavecchia, G.; Blas, J.; López, L.; Tanferna, A.; Hiraldo, F. Variation in age-structured vital rates of a long-lived raptor: Implications for population growth. *Basic Appl. Ecol.* **2011**, *12*, 107–115. [CrossRef]
22. Reed, J.M.; Oring, L.W. Reconnaissance for future breeding sites by Spotted Sandpipers. *Behav. Ecol.* **1992**, *3*, 310–317. [CrossRef]
23. Reed, J.M.; Boulinier, T.; Danchin, E.; Oring, L.W. Informed Dispersal. In *Current Ornithology*; Nolan, V., Ketterson, E.D., Thompson, C.F., Eds.; Springer: Boston, MA, USA, 1999; Volume 19, pp. 189–259. [CrossRef]
24. Schjørring, S.; Gregersen, J.; Bregnballe, T. Prospecting enhances breeding success of first-time breeders in the great cormorant, *Phalacrocorax carbo sinensis*. *Anim. Behav.* **1999**, *57*, 647–654. [CrossRef]
25. Pärt, T.; Arlt, D.; Doligez, B.; Low, M.; Qvarnström, A. Prospectors combine social and environmental information to improve habitat selection and breeding success in the following year. *J. Anim. Ecol.* **2011**, *80*, 1227–1235. [CrossRef] [PubMed]

26. Ponchon, A.; Chambert, T.; Lobato, E.; Tveraa, T.; Grémillet, D.; Boulinier, T. Breeding failure induces large scale prospecting movements in the black-legged kittiwake. *J. Exp. Mar. Biol. Ecol.* **2015**, *473*, 136–145. [CrossRef]
27. Kloskowski, J. Win-stay/lose-switch, prospecting-based settlement strategy may not be adaptive under rapid environmental change. *Sci. Rep.* **2021**, *11*, 570. [CrossRef] [PubMed]
28. Fasciolo, A.; Delgado, M.M.; Cortés, G.; Soutullo, A.; Penteriani, V. Limited prospecting behaviour of juvenile Eagle Owls *Bubo bubo* during natal dispersal: Implications for conservation. *Bird Study* **2016**, *63*, 128–135. [CrossRef]
29. Whitfield, D.P.; Fielding, A.H. *Analyses of the Fates of Satellite Tracked Golden Eagles in Scotland*; SNH Commissioned Report No. 982; SNH: Battleby, UK, 2017.
30. Haller, H. Raumorganisation und dynamik einer population des Steinadlers *Aquila chrysaetos* in den zentralalpen. *Ornithol. Beob.* **1982**, *79*, 163–211.
31. Haller, H. Der Steinadler *Aquila chrysaetos* als Brutvögel im schweizerischen Alpenvorland: Ausbreitungstendenzen und ihre populationsökologischen Grundlagen. *Ornithol. Beob.* **1994**, *91*, 237–254.
32. Johnson, M.L. Exploratory behavior and dispersal: A graphical model. *Can. J. Zool.* **1989**, *67*, 2325–2328. [CrossRef]
33. Millsap, B.A.; Harmata, A.R.; Stahlecker, D.W.; Mikesic, D.G. Natal dispersal distance of bald and golden eagles originating in the coterminous United States as inferred from band encounters. *J. Raptor Res.* **2014**, *48*, 13–23. [CrossRef]
34. Murphy, R.K.; Stahlecker, D.W.; Millsap, B.A.; Jacobson, K.V.; Johnson, A.; Smith, C.S.; Tator, K.J.; Kruse, K.L. Natal dispersal distance of Golden Eagles in the southwestern United States. *J. Fish Wildl. Manag.* **2019**, *10*, 213–218. [CrossRef]
35. Whitfield, D.P.; Fielding, A.H.; Anderson, D.; Benn, S.; Reid, R.; Tingay, R.; Weston, E. Sex difference in natal dispersal distances of Golden Eagles *Aquila chrysaetos* in Scotland. *Ibis* 2023, *in press*.
36. López-López, P. Individual-based tracking systems in ornithology: Welcome to the era of big data. *Ardeola* **2016**, *63*, 103–136. [CrossRef]
37. Hayhow, D.B.; Benn, S.; Stevenson, A.; Stirling-Aird, P.K.; Eaton, M.A. Status of Golden Eagle *Aquila chrysaetos* in Britain. *Bird Study* **2017**, *64*, 281–294. [CrossRef]
38. Whitfield, D.P.; Fielding, A.H.; McLeod, D.R.A.; Haworth, P.F. *A Conservation Framework for Golden Eagles: Implications for Their Conservation and Management in Scotland*; Scottish Natural Heritage Commissioned Report No.193 (ROAME No. F05AC306); SNH: Battleby, UK, 2008.
39. Fielding, A.H.; Haworth, P.; Anderson, D.; Benn, S.; Dennis, R.; Weston, E.; Whitfield, D.P. A simple topographical model to predict Golden Eagle *Aquila chrysaetos* space use during dispersal. *Ibis* **2020**, *162*, 400–415. [CrossRef]
40. Fielding, A.H.; Anderson, D.; Benn, S.; Dennis, R.; Geary, M.; Weston, E.; Whitfield, D.P. Responses of dispersing GPS-tagged Golden Eagles *Aquila chrysaetos* to multiple wind farms across Scotland. *Ibis* **2022**, *164*, 102–117. [CrossRef]
41. Watson, J. *The Golden Eagle*, 2nd ed.; Poyser: London, UK, 2010.
42. Whitfield, D.P.; MacLeod, D.R.A.; Watson, J.; Fielding, A.H.; Haworth, P.F. The association of grouse moor in Scotland with the illegal use of poisons to control predators. *Biol. Conserv.* **2003**, *114*, 157–163. [CrossRef]
43. Whitfield, D.P.; Fielding, A.H.; McLeod, D.R.A.; Haworth, P.F. The effects of persecution on age of breeding and territory occupation in golden eagles in Scotland. *Biol. Conserv.* **2004**, *118*, 249–259. [CrossRef]
44. Whitfield, D.P.; Fielding, A.H.; McLeod, D.R.A.; Haworth, P.F. Modelling the effects of persecution on the population dynamics of golden eagles in Scotland. *Biol. Conserv.* **2004**, *119*, 319–333. [CrossRef]
45. Whitfield, D.P.; Fielding, A.H.; McLeod, D.R.A.; Haworth, P.F.; Watson, J. A conservation framework for the golden eagle in Scotland: Refining condition targets and assessment of constraint influence. *Biol. Conserv.* **2006**, *130*, 465–480. [CrossRef]
46. Whitfield, D.P.; Fielding, A.H.; McLeod, D.R.A.; Morton, K.; Stirling-Aird, P.; Eaton, M.A. Factors constraining the distribution of Golden Eagles *Aquila chrysaetos* in Scotland. *Bird Study* **2007**, *54*, 199–211. [CrossRef]
47. Whitfield, D.P.; Benn, S.; Grant, J.R.; Weston, E. The diet of breeding Golden Eagles in the Central Highlands of Scotland. *Scot. Birds* **2022**, *42*, 202–209.
48. Watson, A.; Wilson, J.D. Seven decades of mountain hare counts show severe declines where high-yield recreational game bird hunting is practised. *J. Appl. Ecol.* **2018**, *55*, 2263–2272. [CrossRef]
49. Watson, J.; Fielding, A.H.; Whitfield, D.P.; Broad, R.A.; Haworth, P.; Nellist, K.; Crane, K.; Macdonald, E.J. Golden eagle breeding performance in relation to climate in western Scotland during the period 1981. In *Birds of Prey in a Changing Environment*; Thompson, D.B.A., Redpath, S., Fielding, A.H., Marquiss, M., Galbraith, C.A., Eds.; The Stationery Office: Edinburgh, UK, 2003; pp. 149–161.
50. Whitfield, D.P.; Reid, R.; Haworth, P.F.; Madders, M.; Marquiss, M.; Tingay, R.; Fielding, A.H. Diet specificity is not associated with increased reproductive performance of Golden Eagles *Aquila chrysaetos* in western Scotland. *Ibis* **2009**, *151*, 255–264. [CrossRef]
51. Fielding, A.H.; Anderson, D.; Benn, S.; Dennis, R.; Geary, M.; Weston, E.; Whitfield, D.P. Non-territorial GPS-tagged golden eagles *Aquila chrysaetos* at two Scottish wind farms: Avoidance influenced by preferred habitat distribution, wind speed and blade motion status. *PLoS ONE* **2021**, *16*, e0254159. [CrossRef] [PubMed]
52. Hoechlin, D.R. Development of golden eaglets in southern California. *West. Birds* **1976**, *7*, 137–152.
53. Peterson, D. *Möt Kungsörnen*; ICA Bokförlag: Västerås, Sweeden, 1997.
54. Phillips, R.A.; Xavier, J.C.; Croxall, J.P. Effects of satellite transmitters on albatrosses and petrels. *Auk* **2003**, *120*, 1082–1090. [CrossRef]
55. Kenward, R.E. *A Manual for Wildlife Radio Tagging*; Academic Press: London, UK, 2001.

56. Sergio, F.; Tavecchia, G.; Tanferna, A.; López Jiménez, L.; Blas, J.; De Stephanis, R.; Marchant, T.A.; Kumar, N.; Hiraldo, F. No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning and condition of its offspring. *J. Appl. Ecol.* **2015**, *52*, 1665–1675. [CrossRef]
57. Davies, M.; Green, R. A classification of methods used to attach devices to vultures and condors. *Vulture News* **2020**, *78*, 12–17. [CrossRef]
58. Orr-Ewing, D.; Anderson, D.; Weston, E. Thoracic X-Strap Harness. Design and Method. *Vulture News* **2020**, *78a*, 27–30. [CrossRef]
59. Thaxter, C.B.; Ross-Smith, V.H.; Clark, J.A.; Clark, N.A.; Conway, G.J.; Masden, E.; Wade, H.M.; Leat, E.H.K.; Gear, S.C.; Marsh, M.; et al. Contrasting effects of GPS device and harness attachment on adult survival of Lesser Black-backed Gulls *Larus fuscus* and Great Skuas *Stercorarius skua*. *Ibis* **2016**, *158*, 279–290. [CrossRef]
60. García, V.; Iglesias-Lebrija, J.J.; Moreno-Opo, R. Null effects of Garcelon harnessing method and transmitter type on soaring raptors. *Ibis* **2021**, *163*, 899–912. [CrossRef]
61. Anderson, D.; Arkumarev, V.; Bildstein, K.; Botha, A.; Bowden, C.G.R.; Davies, M.; Duriez, O.; Forbes, N.A.; Godino, A.; Green, R.E.; et al. Practical guide to methods for attaching research devices to vultures and condors. *Vulture News* **2020**, *78a*, 1–72, IUCN Species Survival Commission Vulture Specialist Group Technical Publication No.1.
62. Calenge, C. The package adehabitat for the R software package: A tool for the analysis of space and habitat use by animals. *Ecol. Model.* **2006**, *197*, 516–519. [CrossRef]
63. Silva, R.; Afán, I.; Gil, J.A.; Bustamante, J. Seasonal and circadian biases in bird tracking with solar GPS-tags. *PLoS ONE* **2017**, *12*, e0185344. [CrossRef] [PubMed]
64. Thieurmel, B.; Elmarhraoui, A. *Suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase*, R Package Version 0.5.0. 2019.
65. Burnham, K.P.; Anderson, D.R. *Model Selection and Inference: A Practical Information-Theoretic Approach*, 2nd ed.; Springer: New York, NY, USA, 2002.
66. Ens, B.J.; van de Pol, M.; Goss-Custard, J.D. The study of career decisions: Oystercatchers as social prisoners. *Adv. Stud. Behav.* **2014**, *46*, 343–419.
67. Murgatroyd, M.; Roos, S.; Evans, R.; Sansom, A.; Whitfield, D.P.; Sexton, D.; Reid, R.; Grant, J.; Amar, A. Sex-specific patterns of reproductive senescence in a long-lived reintroduced raptor. *J. Appl. Ecol.* **2018**, *87*, 1587–1599. [CrossRef] [PubMed]