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ORIGINAL PAPER

Sensitivity of Adélie and Gentoo penguins to various flight activities of a micro UAV

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Abstract

A recent increase in the use of unmanned aerial vehicles (UAVs)—also known as remotely piloted aircraft (RPA)—in the Antarctic in private, commercial and scientific sectors suggests that operational guidelines are urgently needed. One of the factors inhibiting adoption of such guidelines is the lack of knowledge about the impact of UAVs on wildlife. During the austral summer field season of 2014/15, data were gathered on the behavioural reactions to UAVs of Gentoo (*Pygoscelis papua*) and Adélie penguins (*Pygoscelis adeliae*), both resident breeding species on Ardley Island, King George Island, South Shetland Islands. A series of overflights at different altitudes above the nesting penguins were conducted with a small octocopter UAV, and their behaviour was recorded by video. Penguin behaviour altered as a result of the UAV flights, and behavioural reactions were more pronounced when the UAV was flown at lower altitudes. In Adélie penguins, behavioural reactions caused by the UAV were evident at the highest tested altitude of 50 m, while in Gentoo penguins reactions were evident from 30 m downwards. For both species, the reactions increased markedly when the UAV was flown at low altitudes of 10–20 m. Gentoo penguins showed significant reactions when the UAV was launched at distances closer than 20 m. There was some evidence of habituation to the UAV at some altitudes for horizontal flights, but no evidence of habituation in vertical flights.

Keywords Adélie penguin · Gentoo penguin · Remotely piloted aircraft · Unmanned aerial vehicle · Disturbance · Behavioural analysis

Introduction

A strong increase in the use of unmanned aerial vehicles (UAVs)—also known as remotely piloted aircraft (systems) (RPA(S)), unmanned aerial systems (UAS), or drones—has been observed all over the world in recent years. Drone sales have increased in both military and private sectors (Cavoukian 2012; Peasgood and Valentin 2015). Included in the latter are professional television and movie productions as well as private enthusiasts, but there are also increasing scientific applications. Studies using drones for biological monitoring are already numerous and include surveys on birds and whales (Koski et al. 2009; Dulava et al. 2015; Durban et al. 2016), surveys on terrestrial mammals (Israel 2011; Vermeulen et al. 2013; Chrétien et al. 2016) and counting of flocks or colonies of birds on land (Grenzdörffer 2013; Liu et al. 2015).

The same general trend is also taking place in the Antarctic. Scientific topics of interest are varied: for example, non-biological applications include iceberg observations and glaciology (McGill et al. 2011; Bhardwaj et al. 2016), while biological applications include vegetation studies (Lucieer et al. 2012) and monitoring of Antarctic animals (Mustafa et al. 2014; Goebel et al. 2015; Ratcliffe et al. 2015). For penguins (or other seabirds), UAVs offer scientists new opportunities to acquire high-resolution images that enable numbers of breeding pairs to be determined in colonies that are too large or too remote to count by conventional methods (e.g. manual ground count, GPS-based ground mapping, and

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photography counts). Even in well-studied colonies, drones can improve on conventional methods by shortening field work duration, achieving better repeatability and higher accuracy of results, and by reducing potential impacts on animals (Mustafa et al. 2017). While some forms of disturbance are reduced when using drones, studies of disturbance by UAVs themselves remain relatively few (Mulero-Pázmány et al. 2017).

Anthropogenic disturbance of animals has been of research interest for many years, and a number of studies have focused on the impact of humans as well as piloted aircraft on breeding birds (Thomson 1977; Hockey and Hallinan 1981; Wilson et al. 1989; Fraser and Patterson 1997; Carney and Sydeman 1999; Giese and Riddle 1999; Ellenberg et al. 2006). The definition of 'disturbance' or 'disturbed' has been used differently, although most of these studies considered 'disturbance' to be indicated by a deviation in heart rate or behaviour from levels typical in a control group that is not subjected to the stimulus of interest. According to this definition, anthropogenic 'disturbance' does not necessarily exceed the stress levels generated by natural stimuli such as predators or lead to actual fitness consequences.

Previous studies of disturbance have led to the establishment of guidelines (not only for penguins, but for all Antarctic wildlife species) for humans approaching animals and for separation distances for piloted aircraft near concentrations of birds (Harris 2005). The general aim of these guidelines is to ensure that, at a minimum, stress levels in animals caused by human activities remain within the range of typical natural stress levels, and ideally at a level that would be considered unstressed. In this study, we follow this commonly used approach for defining when a bird is 'disturbed'.

The environmental aspects of UAV use in Antarctica have been considered by the Committee for Environmental Protection (CEP) and Antarctic Treaty Consultative Meeting (ATCM) for several years (ATCM 2014, 2015, 2018). The Council of Managers of National Antarctic Programs (COMNAP) first presented a manual with guidance for UAS operations in 2016 (COMNAP 2016), although this manual had minimal guidance specifically related to environmental concerns. The CEP recognized the benefit of developing more specific environmental guidance for operating RPAS in Antarctica in 2017 when it established a working group on the topic, which reported back to the 2018 ATCM (Germany 2018).

There have to date been few experimental studies to determine the magnitude of disturbance or significance of impact caused by UAVs on animals to provide a scientifically strong basis for operating guidelines anywhere in the world, let alone in Antarctica. Most studies report observations of animal reactions recorded during their regular monitoring trials (Hanson et al. 2014; Ratcliffe et al. 2015), while some undertake specific experiments to evaluate animal reactions in different flight situations (Ditmer et al. 2015; Pomeroy et al. 2015; Vas et al. 2015; McEvoy et al. 2016).

With respect to penguins, most studies make only behavioural observations of disturbance during UAV surveys (Goebel et al. 2015; Ratcliffe et al. 2015). Goebel et al. (2015) reported no 'signs of disturbance' for penguins when operating an electric UAV at altitudes from 30 to 60 m. Ratcliffe et al. (2015) observed Gentoo penguins (*Pygoscelis papua*) did not abandon nests when operating an electric UAV at flight altitudes of 30 m, although non-breeding individuals were 'walking away' from the drone, highlighting the importance of breeding status in relation to outward behavioural reactions. Korczak-Abshire et al. (2016) reported observations of Adélie penguins (*Pygoscelis adeliae*) during overflights at altitudes of 350 m using fixed wing UAVs of 2–4 m wingspan with different engines. No reactions were observed during overflight of the electric engine UAV, while vigilance was observed during overflight of the piston engine UAV, which generated substantially more noise. Weimerskirch et al. (2018) conducted specific experiments to test the reactions to drones for a variety of Antarctic and Sub-Antarctic seabirds, showing distinct differences between species. In an earlier study, Rümmler et al. (2016) reported measureable changes in the behaviour of Adélie penguins when overflown by an electric UAV even at flight altitudes of 50 m, and that the disturbance caused by the UAV increased significantly in lower altitudes. Similar results were observed in Gentoo penguins (Mustafa et al. 2017).

The current study refines the results in Rümmler et al. (2016) and Mustafa et al. (2017) by analysing penguin behaviour on an individual level in contrast to the group scale previously reported. In addition, a behavioural index will be used to analyse the level of disturbance where applicable, rather than using the more simple binary classification of either 'disturbed' or 'undisturbed'. This approach allows the magnitude of disturbance to be taken into account. Additional experiments were undertaken to assess the influence of launch site distances on Gentoo penguins. Finally, the influence of short-term habituation and seasonality on penguin behavioural reactions will be evaluated by statistical analysis.

Methods

Study site

Data collection took place at a mixed colony of Adélie, Gentoo and chinstrap (*Pygoscelis antarctica*) penguins during the austral summer field season of 2014/15 on Ardley Island, King George Island, South Shetland Islands (Braun et al.

2012). Ardley Island is designated as an Antarctic Specially Protected Area and entry to the breeding site is prohibited without a permit. Four breeding groups were selected for study, two of Adélie and two of Gentoo penguins (Fig. 1). Two of the breeding groups were situated on a plateau at about 30 m a.s.l. (above sea level) and the other two were located near the northern coastline at about 10 m a.s.l. Breeding groups were selected at the maximal distance possible from each other, within topographical constraints, in order to minimize the potential for experiments on one group to affect any other. In general, because it is impractical to distinguish individual penguins, it was impossible to control which adult was present at the nest on different investigation days. Heavy snowfalls at the beginning of December led to substantial nest losses in Adélie breeding Group 2 (A2, Fig. 1), and this group had to be excluded from the study afterwards. Chinstrap penguins were not included in the study because of the small number of breeding pairs present and their preference to breed on rocks in areas unsuitable for the UAV trials.

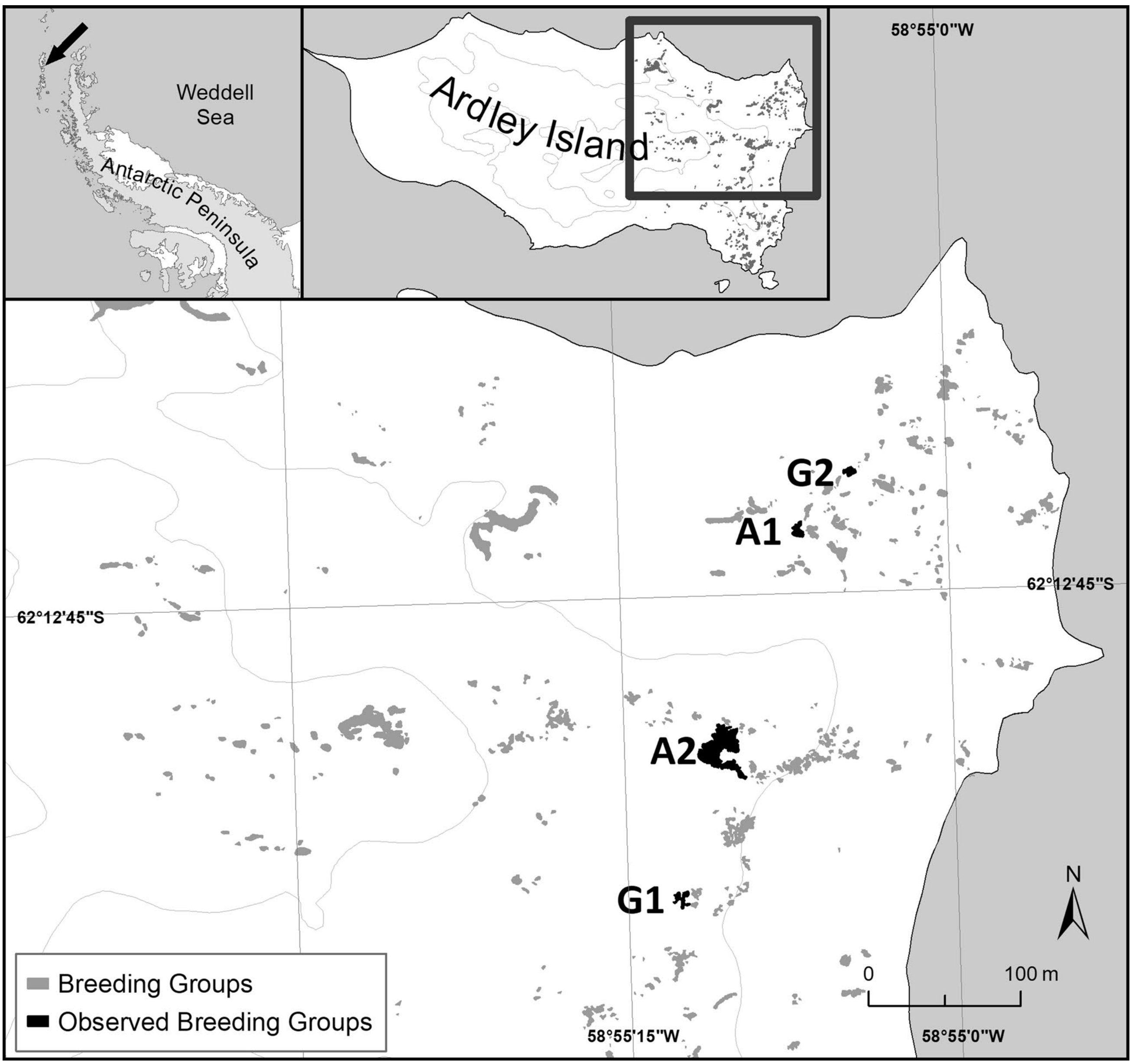

Fig. 1 Location of the study area and observed breeding groups within the colony on Ardley Island. Marked are the observed breeding groups of Adélie penguins (A1, A2, *Pygoscelis adeliae*) and the observed breeding groups of Gentoo penguins (G1, G2, *Pygoscelis papua*). Breeding groups A1 and G2 are located on the beach terrace. Breeding groups A2 and G1 are located on a plateau on a higher ground level

UAV specifications

Like in previous studies (Rümmler et al. 2016; Mustafa et al. 2017), an Octocopter MK ARF Okto XL (HiSystems) with a total weight of 3.5 kg (incl. batteries) in flight configuration was used for this study. The maximum size of the microcopter is 73 × 73 × 36 cm, and it emits a noise level of 70 dB at a distance of 5 m (pers. com. HiSystems). According to Brown (2008), the noise level decreases by 6 dB with a doubling of the distance from the source. Therefore, the noise level at 40-m distance is assumed to be 52 dB. However, the actual noise level at any distance varies due to the influence of weather, terrain and the position and flight direction of the UAV. These variables were not measured in the study. Equipped with GPS and an inertial measurement unit (IMU), the UAV has autonomous flight capability, which was used for the flight schemes to ensure precise repetition of the experimental positioning and flight-speed settings while conducting the multiple runs. During the flights, the UAV was not equipped with any camera or sensor.

Flight schemes

Two general flight schemes were applied to test the influence that UAVs have on nesting penguins when flying at different altitudes and directions (Fig. 2). In both flight modes, the UAV was launched from a take-off point 20–50 m from the focal group. This distance varied between the investigated breeding groups as a result of local conditions, such as rocks blocking the way or other close breeding groups being potentially disturbed. After launch, the UAV travelled to the first waypoint of the GPS-based programmed track at 50 m a.g.l. (above ground level), which in the case of horizontal flights was positioned approximately 50 m from the centre of the focal group. From this first waypoint, overflight transects were conducted at constant altitudes (50, 40, 30, 25, 20, 15 and 10 m) back and forth in a descending order. Upward vertical movements consume more energy, so an efficient flight plan was needed to save battery power to conduct the necessary number of flights needed for behavioural analysis, which prevented use of a randomized altitude order.

After the last overflight, the UAV maintained its then current altitude to fly away from the breeding group and land remotely, in most cases close to the launch site. The landing is a critical moment in any UAV flight, particularly in windy conditions, and for this reason the landing site could not always be planned in advance. An example of a UAV flight over breeding group G1 is given in Online Resource 1.

In vertical flights, the UAV again travelled to the first waypoint after launch, which was located 50 m above the centre of the focal group. From that position, the UAV lowered down directly towards the penguins until it reached an altitude of 10 m, from where it flew horizontally away from the focal group.

On each observation day (Table 1), both flight schemes were performed three times for each investigated breeding group. Between consecutive flights we waited until all individuals returned to behavioural patterns typically observed before the flight to reduce the possibility of double-counting reactions that were actually produced by the earlier flight. If other sources of potential disturbance like predators, pedestrians or piloted aircrafts were observed the experiment was paused and continued when individuals returned to their typical behavioural patterns.

Take-off experiments were conducted on both Gentoo penguin groups, and only on one observation day, which was a different day to those on which other flight experiments were conducted (Table 1). In those experiments, the UAV was launched vertically at distances of 50, 40, 30, 20, 15, 10, and 5 m from the centre of the focal group, and after reaching an altitude of about 30 m, immediately landed again approximately at the starting point. The UAV was then carried to the next closest take-off point to the centre and launched again (Fig. 2). This scheme was repeated three times per group, again waiting until all individuals returned to their original behaviour before starting the next cycle. During all take-offs, the UAV pilot was positioned close to the UAV to mimic typical scenarios of UAV use. Only the first three seconds of video after take-off were analysed owing to the variable flight behaviour of the UAV that occurred mainly as a result of changes in wind velocity, and the landing process was not analysed.

The mean flight velocity during horizontal flights was 6 ms^{-1}, in vertical flights the UAV descended with a mean speed of 3 ms^{-1}. In the take-off experiments, the mean climb velocity was 3 ms^{-1}.

The focal animals were video-recorded with a standard camera (Panasonic® LUMIX G5®) on a tripod. The video material was analysed using CowLog 2.0 software (Hänninen and Pastell 2009). The behavioural analysis of Adélie penguins was based on the ethogram given in Schuster (2010), while for Gentoo penguins, it was based on descriptions in Jouventin (1982) and Van Zinderen Bakker et al. (1971) and completed with our own observations. Detailed descriptions of the behaviour of both species can be found in (Mustafa et al. 2017). Behaviour was analysed for each clearly visible nesting adult individual of the focal group and described in detail for every second of footage in the recordings. The time (10–242 s, mean 54 s) before the first take-off of each cycle was used as control period. To compare the different behavioural reactions shown by each individual, all behaviours were classified on a scale indicating the strength of their disturbance (Table 2). The ‘disturbance index’ is an ordinal scale and not a metric classification, since natural behaviour cannot be precisely scaled. The purpose of

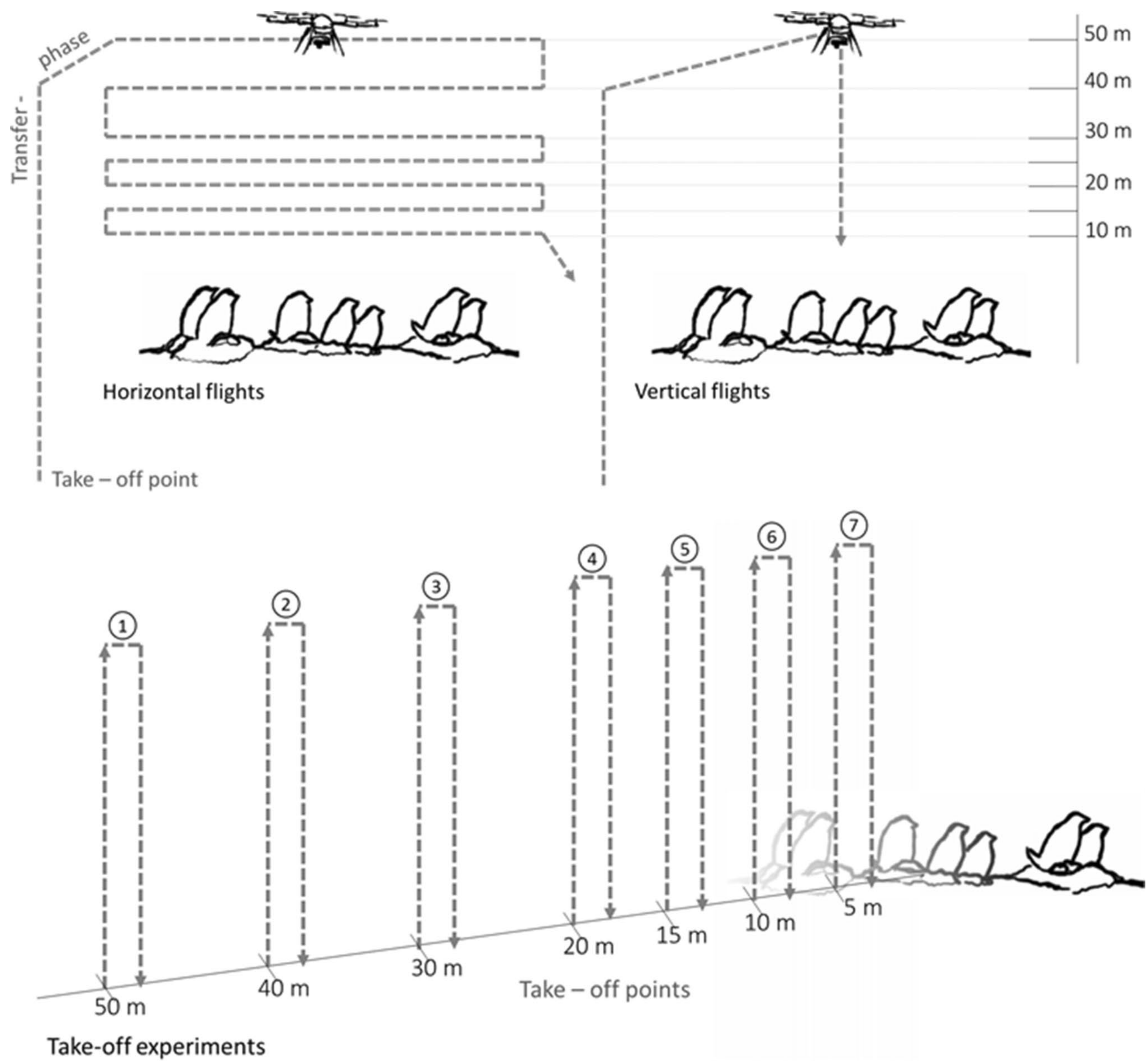

Fig. 2 Flight schemes applied in the experiments. Top: horizontal (left) and vertical (right) flight modes, bottom: take-off experiments. All altitudes are given as meters above ground level of the focal group

the index is to sort different behaviours according to their relative level of disturbance. Thus, an increase from − 1 to 0 on the 'disturbance index' does not necessarily indicate the same magnitude of change in disturbance as an increase from 1 to 2.

Statistics

For statistical analysis, the median of the disturbance index of each second was calculated for each individual penguin in each flight situation (altitude and flight number). In vertical flights, the flight altitudes for each second were grouped to match the altitude levels of horizontal flights (50 m: 50–45 m; 40 m: 44.9–35 m; 30 m: 34.9–27.5 m; 25 m: 27.4–22.5 m; 20 m: 22.4–17.5 m; 15 m: 17.4–12.5 m; and 10 m: 12.4–10 m).

In the analysis of take-off experiments, a median of the disturbance index for the first three seconds after take-off was calculated for each individual and each take-off distance.

Change in UAV flight altitude was the only factor analysed, since previous research showed that wind speed, as the only other measured potentially influential variable, is not an important factor (Rümmler et al. 2016; Mustafa et al. 2017). The Kruskal–Wallis test/Jonckheere-Terpstra test and

Table 1 Overview of the observation dates and the experiments conducted on each day and breeding group (A1, A2, G1, and G2, see Fig. 1). *HF* horizontal flights, *VF* vertical flights, *TE* take-off experiments, *HE* habituation experiments (analysed in Rümmler et al. 2016; Mustafa et al. 2017)

Observation date	Experiment time	Breeding phase	Observed breeding groups			
			Adélie penguins		Gentoo penguins	
			Pygoscelis adeliae		*Pygoscelis papua*	
			A1	A2	G1	G2
11/14/2014	16:30–17:20	Incubation phase	–	HE	–	–
11/23/2014	12:00–15:15		HF/VF	HF/VF	–	–
12/07/2014	15:00–17:15		–	–	HF/VF	HF/VF
12/16/2014	11:15–12:30		–	–	HE	HE
12/29/2014	11:00–14:15		–	–	TE	TE
01/02/2015	10:15–11:50	Chick guarding	HF/VF	–	–	–
01/17/2015	15:30–18:00		HF/VF	–	HF/VF	HF/VF
02/01/2015	16:30–18:00		–	–	HF/VF	HF/VF
02/10/2015	13:10–15:00	Crèche phase	–	–	HF/VF	HF/VF

Table 2 Analysed behaviours of Adélie and Gentoo penguins (*Pygoscelis adeliae/P. papua*) and behavioural classes as also used in Rümmler et al. (2016) and Mustafa et al. (2017), following Van Zinderen Bakker et al. (1971), Jouventin (1982) and Schuster (2010) and own observations. For each behaviour, its indicated disturbance and the following disturbance index used for analyses are provided

Behaviour		Behavioural class	Indicated disturbance	Disturbance index
Adélie penguin	Gentoo penguin			
Ecstatic display	Ecstatic display	Comfort	None	− 2
Mutual display				
Bowing	Bowing			
Both wing stretch	Both wing stretch			
Ruffle shake	Body shake			
Rapid wing flap				
Cleaning/preening	Cleaning/preening			− 1
Manipulation nest/chick	Manipulation nest/chick			
Resting	Sleeping	Resting	None or very low	0
	Low vigilance	Vigilance	Low	1
Vigilance			Low to mediocre	1.5
	High vigilance		Mediocre	2
Bill-to-axilla	Low intensity threat	Agonistic	Mediocre to high	3
Sideways/alternate stare				
Point				
Gape	High intensity threat		High	4
Charge				
Escape	Escape	Escaping	Very high	5

subsequent pairwise comparison by the Bonferroni post hoc test were used for analyses of the impact of different flight altitudes and take-off distances. These analyses were performed in IBM® SPSS® Statistics 22.0.

For analyses of habituation, the mean was calculated per individual and flight altitude, in this case from disturbed/undisturbed categories, with disturbed being composed of vigilance, agonistic and escape behaviours and undisturbed of resting and comfort behaviours (Table 2; Rümmler et al. 2016). By this means it was possible to fit a binomial generalized linear mixed model (GLMM) for each altitude to test for the influence of repetition number on the observed disturbance with observation day, group and individual number (nested in group) as random factors and flight number as fixed factor. These analyses were performed using the lmerTest 2.0-33 package (Kuznetsova et al. 2015) in R 3.3.1 (R Development Core Team 2008) with RStudio 1.0.136 (RStudio Team 2016).

To test for changes of sensitivity between different stages of the breeding cycle, the above described disturbed/undisturbed classification was used again. Two GLMMs were created containing group and individual number (nested in group) as random factors, one including the observation day as a fixed factor, the other without. An ANOVA was then used to test for statistically significant differences between the models, indicating an influence of the observation day.

All graphs were created using Systat Software GmbH SigmaPlot™ 13.0 or R Studio.

Results

The analyses revealed that the UAV flights had a significant influence on the behaviour of the sample groups of Adélie and Gentoo penguins, which indicated increasing disturbance with lower flight altitudes for both species and in both horizontal and vertical flight schemes. A clear shift in behaviour patterns occurs from control levels (no UAV disturbance) to low flight altitudes (Fig. 3). In Adélie penguins, resting is the dominant behaviour in the control phase, while in Gentoo penguins, most individuals displayed low vigilance. With the decreasing flight altitude, vigilant behaviour increases in Adélie penguins and high vigilance in Gentoo penguins. Agonistic and comfort behaviours stay almost constant on a relatively low level during all phases in both species.

The influence of different flight altitudes will be considered now for both species and the flight modes separately in the following section. For each analysis, the cross tables will be provided.

Influence of UAV flight altitude on penguin behaviour

The control (pre-take-off) and transfer (take-off to first waypoint) phases were similar in horizontal and vertical flight schemes, so we tested for differences between the reactions to the UAV in those two flight phases. No significant difference was found in the behavioural reactions between flight schemes in both species (Mann–Whitney-U test; Adélie penguins ($U = 1583$; $p = 0.5923$; $N = 116$); Gentoo penguins ($U = 7010$; $p = 0.7001$; $N = 234$), so the data were pooled to enlarge the sample size for statistical analysis.

The statistical results of the Jonckheere-Terpstra test for the influence of different flight altitudes on the behaviour in different experimental situations are presented in Table 3. In all situations, there were statistically significant differences in the behavioural reactions caused by overflights at different altitudes.

Gentoo penguins

The general pattern of behavioural response was similar in both horizontal and vertical flights for Gentoo penguins. In both flight schemes, at altitudes of 40 m, 50 m and in the transfer phase, there was no significant difference in penguin behaviour than in the control period. There was also no significant difference in penguin behaviours between the transfer phase and when the UAV was operating at altitudes

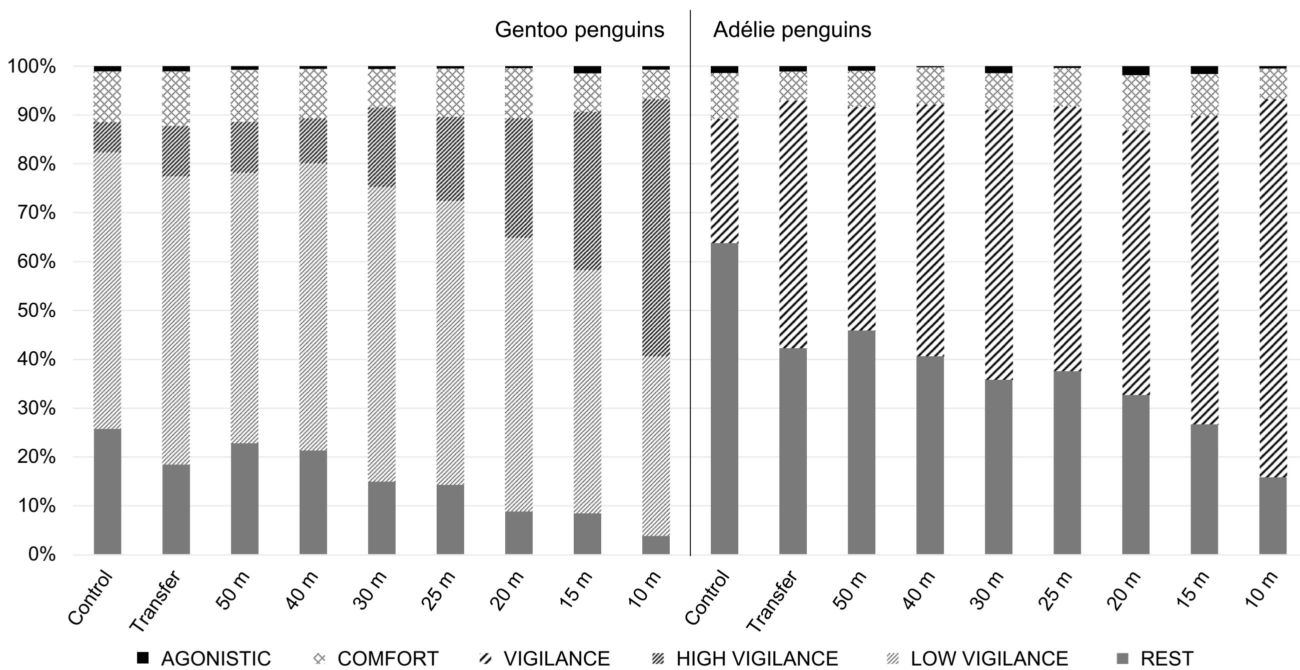

Fig. 3 General overview over the frequency of behavioural classes (see Table 2) in different flight phases for Gentoo and Adélie penguins (*Pygoscelis papua/P. adeliae)*. For Gentoo penguins, the vigilance group was divided into high and low vigilance. Horizontal and vertical data are pooled

above 20 m, except for a very weak difference between 30-m overflights and transfer in horizontal flights (Tables 4, 5). That means that in all tested flight altitudes above 30 m for Gentoo penguins the disturbance is not to be considered significantly increased, but it is indeed observable, since the mean disturbance indices are always higher. At and below 30 m, a gradual increase in disturbance is observed with decreasing altitude. There is evidence of a sudden increase in the reaction of Gentoo penguins to vertical flights at an altitude of 20 m.

Adélie penguins

Reactions that were significantly different from the control period were observed at all flight altitudes for Adélie penguins (Tables 6, 7). In horizontal flights, 10 m overflights were also significantly different from all other flight altitudes. Among the rest, no statistical differences could be found. In vertical flights, 10 m overflights were significantly different from all other altitudes except 15 m, and the reaction to overflights at 15 m altitudes were found to be different from all except 20 m and 25 m. As in Gentoo penguins,

Table 3 Results of the statistical tests for differences in the disturbance index comparing overflights in different flight altitudes above breeding Adélie and Gentoo penguins (*Pygoscelis adeliae/P. papua*) in vertical and horizontal flights

Species	Flight scheme	*T/F*	*p*	*N*
Gentoo penguins	Horizontal Jonckheere-Terpstra test	− 12.286	< 0.0001	1428
	Vertical Jonckheere-Terpstra test	− 15.662	< 0.0001	1394
Adélie penguins	Horizontal Jonckheere-Terpstra test	− 8.125	< 0.0001	807
	Vertical Jonckheere-Terpstra test	− 9.935	0.0002	785
Gentoo penguins	Take-off experiments Kruskal–Wallis test	57.416	< 0.001	336

Table 4 Results of the pairwise comparison (Bonferroni post hoc test) of the disturbance index of Gentoo penguins (*Pygoscelis papua)* during horizontal flights. Upper-right corner: *p* values; lower-left corner: difference of means (column–row). Significant relations are given in bold

	Control	Transfer	50 m	40 m	30 m	25 m	20 m	15 m	10 m
Control		0.8918	1.0000	1.000	**0.0003**	**0.0340**	**< 0.0001**	**< 0.0001**	**< 0.0001**
Transfer	− 0.1197		1.0000	1.000	**0.0431**	1.000	**0.0009**	**< 0.0001**	**< 0.0001**
50 m	− 0.1006	0.0190		1.000	0.0749	1.000	**0.0070**	**< 0.0001**	**< 0.0001**
40 m	− 0.1260	− 0.0063	− 0.0254		0.6178	1.000	**0.0717**	**0.0010**	**< 0.0001**
30 m	− 0.3579	− 0.2382	− 0.2572	− 0.2319		1.000	1.000	0.6229	**< 0.0001**
25 m	− 0.2375	− 0.1178	− 0.1369	− 0.1115	0.1204		1.000	0.0765	**< 0.0001**
20 m	− 0.3760	− 0.2563	− 0.2754	− 0.2500	− 0.0181	− 0.1385		1.000	**< 0.0001**
15 m	− 0.4774	− 0.3578	− 0.3768	− 0.3514	− 0.1196	− 0.2400	− 0.1014		**< 0.0001**
10 m	− 0.9050	− 0.7853	− 0.8043	− 0.7790	− 0.5471	− 0.6675	− 0.5290	− 0.4275	

Table 5 Results of the pairwise comparison (Bonferroni post hoc test) of the disturbance index of Gentoo penguins (*Pygoscelis papua)* during vertical flights. Upper-right corner: *p* values; lower-left corner: difference of means (column−row). Significant relations are given in bold

	Control	Transfer	50 m	40 m	30 m	25 m	20 m	15 m	10 m
Control		0.8918	1.000	1.000	**0.0194**	**0.0008**	**< 0.0001**	**< 0.0001**	**< 0.0001**
Transfer	− 0.1197		1.000	1.000	1.000	0.0811	**< 0.0001**	**< 0.0001**	**< 0.0001**
50 m	− 0.0442	0.0755		1.000	0.9063	0.0946	**< 0.0001**	**< 0.0001**	**< 0.0001**
40 m	− 0.0922	0.0274	− 0.0481		1.000	0.1697	**< 0.0001**	**< 0.0001**	**< 0.0001**
30 m	− 0.2351	− 0.1154	− 0.1909	− 0.1429		1.000	**0.0004**	**< 0.0001**	**< 0.0001**
25 m	− 0.3291	− 0.2094	− 0.2849	− 0.2368	− 0.0940		**0.0370**	**< 0.0001**	**< 0.0001**
20 m	− 0.5885	− 0.4688	− 0.5443	− 0.4962	− 0.3534	− 0.2594		0.3366	**0.0002**
15 m	− 0.7990	− 0.6794	− 0.7548	− 0.7068	− 0.5639	− 0.4699	− 0.2105		0.3155
10 m	− 0.9795	− 0.8598	− 0.9353	− 0.8872	− 0.7444	− 0.6504	− 0.3910	− 0.1805	

Table 6 Results of the pairwise comparison (Bonferroni post hoc test) of the disturbance index of Adélie penguins (*Pygoscelis adeliae*) during horizontal flights. Upper-right corner: *p* values; lower-left corner: difference of means (column–row). Significant relations are given in bold

	Control	Transfer	50 m	40 m	30 m	25 m	20 m	15 m	10 m
Control		**< 0.0001**	**0.0445**	**0.0016**	**< 0.0001**	**0.0001**	**0.0001**	**< 0.0001**	**< 0.0001**
Transfer	– 0.5388		1.000	1.000	1.000	1.000	1.000	1.000	**< 0.0001**
50 m	– 0.3372	0.2016		1.000	0.0960	1.000	1.000	0.3396	**< 0.0001**
40 m	– 0.4576	0.0812	– 0.1204		0.9426	1.000	1.000	1.000	**< 0.0001**
30 m	– 0.7168	– 0.1780	– 0.3796	– 0.2593		1.000	1.000	1.000	**0.0147**
25 m	– 0.5502	– 0.0114	– 0.2130	– 0.0926	0.1667		1.000	1.000	**0.0002**
20 m	– 0.5718	– 0.0330	– 0.2346	– 0.1142	0.1451	– 0.0216		1.000	**0.0006**
15 m	– 0.6397	– 0.1009	– 0.3025	– 0.1821	0.0772	– 0.0895	– 0.0679		**0.0045**
10 m	– 1.0841	– 0.5453	– 0.7469	– 0.6265	– 0.3673	– 0.5340	– 0.5123	– 0.4444	

Table 7 Results of the pairwise comparison (Bonferroni post hoc test) of the disturbance index of Adélie penguins (*Pygoscelis adeliae*) during vertical flights. Upper-right corner: *p* values; lower-left corner: difference of means (column–row). Significant relations are given in bold

	Control	Transfer	50 m	40 m	30 m	25 m	20 m	15 m	10 m
Control		**< 0.0001**	**0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**
Transfer	– 0.5388		1.000	1.000	1.000	1.000	1.000	**0.0079**	**< 0.0001**
50 m	– 0.5202	0.0185		1.000	1.000	1.000	0.9917	**0.0064**	**< 0.0001**
40 m	– 0.5720	– 0.0332	– 0.0517		1.000	1.000	1.000	**0.0219**	**0.0001**
30 m	– 0.5752	– 0.0364	– 0.0549	– 0.0032		1.000	1.000	**0.0410**	**0.0002**
25 m	– 0.6543	– 0.1155	– 0.1340	– 0.0823	– 0.0791		1.000	0.2047	**0.0014**
20 m	– 0.7017	– 0.1629	– 0.1815	– 0.1297	– 0.1266	– 0.0475		1.000	**0.0253**
15 m	– 0.9612	– 0.4224	– 0.4410	– 0.3892	– 0.3861	– 0.3070	– 0.2595		1.000
10 m	– 1.0973	– 0.5585	– 0.5771	– 0.5253	– 0.5222	– 0.4430	– 0.3956	– 0.1361	

a sudden increase in the reaction can be seen at 15 m (vertical flights) and 10 m (horizontal flights). Also, the reaction to vertical flights below 20 m is again higher than that to horizontal flights. In contrast to Gentoo penguins, Adélie penguin reactions during the transfer phase were always significantly different from the control group.

The boxplots for all flight situations can be found in Online Resource 2.

Influence of different take-off distances

There were statistical differences between the examined take-off distances (Table 3). The post hoc test (Table 8) showed significant differences between launches at 5 m distance and all other distances (including control) except 10 and 15 m. Take-off at a 10 m distance caused significantly higher reactions than take-offs at 30 m and 50 m, as well as the control phase. There were no significant differences between all other distances. The boxplots can be seen in Online Resource 3.

Examination of habituation

Habituation was not observed in vertical flights at all, although the plotted results (see Online Resource 4) seem to indicate some habituation in Gentoo penguins at least at 50 m and 40 m. Between repeated horizontal flights the flight number had a significant influence on the reactions of Adélie and Gentoo penguins when all flight altitudes were pooled (see Table 9). In horizontal flights over Adélie penguins, disturbance shows a tendency to decline with flight number at every altitude except 10 m (see Online Resource 4), but habituation was found to be statistically significant only in high altitudes (50 and 40 m) and at 15 m. In Gentoo penguins, habituation was statistically proven in the single altitudes of 25 m and 10 m, and a decline can be seen at those altitudes in the boxplots (Online Resource 4).

Examination of seasonal differences

In Gentoo penguins, behavioural reactions to overflights were not significantly influenced by the timing of the observation

Table 8 Cross table of the pairwise comparison (Bonferroni post hoc test) of the disturbance index of Gentoo penguins (*Pygoscelis papua*) during take-offs at different distances. Upper-right corner: *p* values; lower-left corner: difference of means (column–row). Significant relations are given in bold

	Control	50 m	40 m	30 m	20 m	15 m	10 m	5 m
Control		1.000	1.000	1.000	1.000	0.4352	**0.0312**	**< 0.0001**
50 m	0.12		1.000	1.000	1.000	0.0743	**0.0034**	**< 0.0001**
40 m	− 0.02	− 0.14		1.000	1.000	0.7286	0.0606	**< 0.0001**
30 m	0.10	− 0.02	0.12		1.000	0.0757	**0.0034**	**< 0.0001**
20 m	− 0.12	− 0.24	− 0.10	− 0.21		1.000	0.6129	**0.0017**
15 m	− 0.31	− 0.43	− 0.29	− 0.40	− 0.19		1.000	0.2917
10 m	− 0.45	− 0.57	− 0.43	− 0.55	− 0.33	− 0.14		1.0000
5 m	− 0.76	− 0.88	− 0.74	− 0.86	− 0.64	− 0.45	− 0.31	

Table 9 Analysis of habituation to repeated UAV flights and the influence of seasonality on the reaction of Adélie and Gentoo penguins (*Pygoscelis adeliae/P. papua*). Shown are the results of the GLMMs with data from disturbed/undisturbed behavioural categories. Significant relations are given in bold. For habituation analysis, all altitudes have been tested separately as well as pooled, seasonality was analysed only with pooled data

Altitude	Gentoo penguins				Adélie penguins			
	Horizontal		Vertical		Horizontal		Vertical	
	Estimate	*p* value	Estimate	*p* value	Estimate	*p* value	Estimate	*p* value
Habituation analysis								
All	**− 0.1892**	**< 0.0001**	− 0.0852	0.1150	**− 0.3115**	**< 0.0001**	− 0.0529	0.3870
50 m	− 0.1647	0.1495	− 0.0874	0.4724	**− 0.4372**	**0.0080**	− 0.1814	0.2514
40 m	− 0.2039	0.0932	− 0.1833	0.1291	**− 0.4349**	**0.0086**	− 0.1994	0.2172
30 m	0.0078	0.9545	− 0.1014	0.4225	− 0.2739	0.0660	0.0442	0.7503
25 m	**− 0.2902**	**0.0285**	− 0.1096	0.4068	− 0.2377	0.0975	0.1450	0.3257
20 m	− 0.1045	0.4518	0.0744	0.6515	− 0.1420	0.2985	− 0.0133	0.9293
15 m	− 0.0261	0.8697	0.0672	0.7691	**− 0.3097**	**0.0337**	0.0164	0.9273
10 m	**− 0.4771**	**0.0445**	− 0.2309	0.4439	− 0.0207	0.9156	− 0.0187	0.9535
χ^2		*p* value	χ^2	*p* value	χ^2	*p* value	χ^2	*p* value
Seasonality analysis								
3.3587		0.3396	0.6778	0.8784	7.9612	**0.0187**	0.4732	0.7893

day over the season. In Adélie penguins, reactions in response to horizontal overflights significantly declined with observation day. There was no significant relationship between reactions and observation day in vertical flights (Table 9). The boxplots can be seen in Online Resource 5.

Discussion

The findings of this study confirm the general trends reported in Rümmler et al. (2016) and Mustafa et al. (2017). The new analysis has revealed that disturbance increases in a more graduated way than previously known.

The results for horizontal overflights demonstrate that Adélie and Gentoo penguins display a pattern of increasingly agitated behavioural response to UAVs as altitudes are reduced, and that reactions increase more substantially when altitudes of ~ 10–20 m are attained. In vertical flights, a substantial increase in agitated behaviour is observed at higher altitudes, suggesting the UAV is perceived as a threat earlier than that in horizontal flights. The higher level of disturbance caused by vertical UAV approaches was also observed in Vas et al. (2015).

For Adélie penguins, already higher flight altitudes were significantly more disturbing than those for the control, whereas in Gentoo penguins, only the influence of low altitudes was confirmed statistically. This suggests that Adélie penguins perceive UAVs earlier than Gentoo penguins. In addition, a significant difference between control and transfer was only observed in Adélie penguins, which lends support to the finding in Mustafa et al. (2017) that Adélie penguins are more sensitive to UAV launches.

The reaction to the UAV shows a distinct increase for both species at a low altitude at 20 m in Gentoo penguins and 15 m/10 m (vertical/horizontal flights) in Adélie penguins. We assume that at this altitude the penguins start regarding the UAV a threat instead of a more observational attitude in higher altitudes. Müller-Schwarze and Müller-Schwarze (1977) observed in experiments with skua dummies and Adélie penguins that the predators were ignored at altitudes of 14 m and higher. By comparison to those observations, the UAV appears to be considered a greater threat by Adélie penguins than this natural source of disturbance, since reactions are initiated at a higher altitude. This could be explained by UAV noise, which is a lot louder than the sound of a skua overflight, even at lower altitudes, or the fact that a UAV is a new and unfamiliar stimulus. However, caution is needed in this comparison because behavioural observations can be very subjective, and the exact observational method (duration and intensity of observations) was not given by the authors.

The take-off sensitivity experiment carried out on Gentoo penguins revealed reactions to UAV launches at distances of 5–15 m. No significant reactions were observed further away, though the boxplots (Online Resource 3) indicate a change in the behaviour already at 20 m. The statistical results suggest that a take-off distance of at least 20 m is appropriate for Gentoo penguins, and incorporating the boxplots leads to a distance of 30 m. The observed disturbance levels in the take-off experiments were unexpectedly low in comparison to the control phase, but also were low in comparison to the equivalent levels of transfer phases in the overflight experiments. The cause of this result is not known, although it is possible that natural variation in behaviour of individuals may have been a factor, which could have arisen as a result of the rather small sample size. Although no take-off experiments were conducted on Adélie penguins, we assume that the appropriate distance is farther since the reaction observed in the transfer phase was stronger.

There was no clear evidence for habituation during repeated overflights at 10 m altitude observed in Rümmler et al. (2016) and Mustafa et al. (2017). However, since the disturbance caused by flights at higher altitudes is lower than that at 10 m, a habituation effect at the high altitude remains conceivable, which was indeed observed in horizontal flights. The finding of a habituation in horizontal flights at 10 m altitude in Gentoo penguins contrasts to the missing habituation in the habituation experiments in Mustafa et al. (2017) at the same altitude. Here, the difference between repeated uninterrupted overflights and several single overflights with a time gap in between seems to be important for habituation.

The observed reduction in reactions by Adélie penguins over the course of the season (Online Resource 5) could point towards a change in sensitivity as chicks begin to merge into the crèche phase and become more independent. At this stage, parents may be less vigilant than was necessary earlier because chicks have become sufficiently mature to be relatively safe from predators. However, this relationship was not actually proven, and hence, there is a need for caution. Other possible reasons for the decline could be weather conditions influencing the visibility or noise level of the UAV, or other natural factors such as predator activity that we did not investigate.

It is important to note that all results discussed here are only valid for the specific model tested. Differences in UAV attributes such as size, colour, shape, noise emissions and flight velocity can have an important influence on penguin reactions. Personal observations and reports from other scientists using UAVs suggest that bird reactions are elevated at moments of strong noise emission, e.g. due to wind gusts or sudden movements of the UAV. It appears that acoustic rather than visual characteristics of the UAV are more influential in the level of disturbance caused, although this aspect was not investigated in this study. This is also supported by findings by Korczak-Abshire et al. (2016). In their experiments, reactions were only observed to the louder piston engine UAV, although the flight altitude was a lot higher than that in our study.

Weimerskirch et al. (2018) surveyed a range of species, of which the macaroni penguin *(Eudyptes chrysolophus)*, rock-hopper penguin *(Eudyptes chrysocome)* and Gentoo penguin are best compared with this study. Macaroni and Gentoo penguin were reported to show comfort or resting behaviour at flight altitudes above 10 m and increased agonistic behaviour below, whereas rock-hopper penguins remained relatively calm, only showing increased stress behaviour at 3-m flight altitudes. The size and noise level of the DJI Phantom UAV used in the experiments may explain the reduced reactions reported here than we observed. However, Weimerskirch et al. (2018) in their study observed bird reactions on-site rather than by video recording, and it is possible that details and subtle reactions of individuals that were recorded as 'disturbance' in our study were missed and thus under-reported.

Multiple factors can have an influence on the susceptibility of individuals or breeding groups to disturbance, such as the size of the breeding group, the frequency of visits from predators, the daily conditions (for example weather or nutritional status and thus energy availability) or the point of time within the breeding phase. The proximity of human activities such as visits by tourists or investigators, or aircraft flying overhead, may also influence bird susceptibility. Those factors were not examined in detail due to the limitations in investigation size but have the potential of altering the behavioural reactions to disturbances. This study was conducted at only one colony, and there is a need for further research on the comparability of results to other penguin nesting sites.

These findings represent only first steps towards understanding the influence of UAVs on penguins, and wildlife in general. Further questions to investigate in future studies include determining the height at which UAV flights over Adélie penguins first cause reactions, experiments to determine the influence of take-offs on Adélie penguins, experiments with different UAV models to understand the influence of their characteristics and experiments on physiological parameters. In particular, it should be noted that the consequential impacts of changes in behavioural reactions in birds, such as implications for individual bird energetics, health, or survival, and the impacts at a colony, population or species level have not been investigated. While we have highlighted behavioural reactions in a number of scenarios for several species, there remains a lack of understanding of the significance of these changes, and this should be paid more research attention.

Conclusions

Observations of wildlife reactions to UAVs in a range of studies suggest that operational guidelines for UAVs would be of benefit to help protect penguins, or wildlife in general, from potential disturbance. Our results suggest the following conclusions with implications for guidelines.

For Gentoo penguins, disturbance is unlikely at flight altitudes of 40 m and above. For Adélie penguins, the precise altitude at which disturbance ceases above 50 m is unknown. An increase in disturbance occurs in both species at flight altitudes below 20 m. Whether this increase in disturbance has consequences for the fitness, including any longer-term population impacts, cannot be evaluated with the data gathered here. The results showed there was no significant increase in penguin escape behaviour leading to deserted nests, suggesting that UAV operations as conducted, even at lower altitudes, are unlikely to have direct impacts on offspring survival. For Gentoo penguins, take-off distances of > 20 m can be expected to avoid disturbance. For Adélie penguins, this distance is expected to be greater but remains unknown.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The study was commissioned by the German Environment Agency, Dessau-Rosslau. All applicable international, national and/or institutional guidelines for the care and use of animals were followed. Permissions to enter ASPA No. 150 were given by the responsible authority.

Informed consent Informed consent was obtained from all individual participants included in the study.

References

ATCM (2014) Final Report of the Thirty-seventh Antarctic Treaty Consultative Meeting Vol 1. Secretariat of the Antarctic Treaty, Brasilia, Brazil

ATCM (2015) Final Report of the Thirty-eighth Antarctic Treaty Consultative Meeting Vol 1. Secretariat of the Antarctic Treaty, Sofia, Bulgaria

ATCM (2018) Final Report of the Forty-first Antarctic Treaty Consultative Meeting—preliminary version Vol 1. Secretariat of the Antarctic Treaty, Buenos Aires, Argentina

Bhardwaj A, Sam L, Martín-Torres FJ, Kumar R (2016) UAVs as remote sensing platform in glaciology: present applications and future prospects. Remote Sens Environ 175:196–204. https://doi.org/10.1016/j.rse.2015.12.029

Braun C, Mustafa O, Nordt A, Pfeiffer S, Peter H-U (2012) Environmental monitoring and management proposals for the Fildes region (King George Island, Antarctica). Polar Res 31:18206. https://doi.org/10.3402/polar.v31i0.18206

Brown P (2008) Fundamentals of audio and acoustics. In: Ballou G (ed) Handbook for sound engineers, 4th edn. Elsevier Focal Press, Amsterdam, pp 21–40

Carney KM, Sydeman WJ (1999) A review of human disturbance effects on nesting colonial waterbirds. Waterbirds 22(1):68–79

Cavoukian A (2012) Privacy and drones: unmanned aerial vehicles. Information and Privacy Commissioner of Ontario, Ontario

Chrétien L-P, Théau J, Ménard P (2016) Visible and thermal infrared remote sensing for the detection of white-tailed deer using an unmanned aerial system. Wildl Soc Bull 40:181–191. https://doi.org/10.1002/wsb.629

COMNAP (2016) Antarctic unmanned aerial systems (UAS) operator's handbook. Prepared by the COMNAP UAS Working Group. https://www.comnap.aq/Groups/Air/SharedDocuments/2Handbookdraft431March2016.pdf. Accessed 25 May 2018

Ditmer MA, Vincent JB, Werden LK, Tanner JC, Laske TG, Iaizzo PA, Garshelis DL, Fieberg JR (2015) Bears show a physiological but limited behavioral response to unmanned aerial vehicles. Curr Biol 25:2278–2283. https://doi.org/10.1016/j.cub.2015.07.024

Dulava S, Bean WT, Richmond OMW (2015) Environmental reviews and case studies: applications of unmanned aircraft systems (UAS) for waterbird surveys. Environ Pract 17:201–210. https://doi.org/10.1017/S1466046615000186

Durban JW, Moore MJ, Chiang G, Hickmott LS, Bocconcelli A, Howes G, Bahamonde PA, Perryman WL, LeRoi DJ (2016)

Photogrammetry of blue whales with an unmanned hexacopter. Mar Mamm Sci. https://doi.org/10.1111/mms.12328
Ellenberg U, Mattern T, Seddon PJ (2006) Physiological and reproductive consequences of human disturbance in Humboldt penguins: the need for species-specific visitor management. Biol Cons 133(1):95–106
Fraser WR, Patterson DL (1997) Human disturbance and long-term changes in Adelie penguin populations: a natural experiment at Palmer Station, Antarctic Peninsula. In: Battaglia B (ed) Antarctic communities, species, structure and survival. University Press, Cambridge, pp 445–452
Germany (2018) Environmental guidelines for operation of remotely piloted aircraft systems (RPAS) in Antarctica. ATCM XLI, Buenos Aires
Giese M, Riddle M (1999) Disturbance of emperor penguin *Aptenodytes forsteri* chicks by helicopters. Polar Biol 22:366–371
Goebel ME, Perryman WL, Hinke JT, Krause DJ, Hann NA, Gardner S, LeRoi DJ (2015) A small unmanned aerial system for estimating abundance and size of Antarctic predators. Polar Biol 38:619–630. https://doi.org/10.1007/s00300-014-1625-4
Grenzdörffer G (2013) UAS-based automatic bird count of a common gull colony. Int Arch Photogramm Remote Sens Spat Inf Sci. https://doi.org/10.5194/isprsarchives-XL-1-W2-169-2013
Hänninen L, Pastell M (2009) CowLog: open source software for coding behaviors from digital video. Behav Res Methods 41(2):472–476
Hanson L, Holmquist-Johnson CL, Cowardin ML (2014) Evaluation of the Raven sUAS to detect and monitor greater sage-grouse leks within the Middle Park population. Open file report. Reston. https://doi.org/10.3133/ofr20141205
Harris CM (2005) Aircraft operations near concentrations of birds in Antarctica: the development of practical guidelines. Biol Cons 125:309–322. https://doi.org/10.1016/j.biocon.2005.04.002
Hockey PAR, Hallinan J (1981) Effect of human disturbance on the breeding behavior of Jackass Penguins *Spheniscus demersus*. S Afr J Wildl Res 11:59–62
Israel M (2011) A UAV-based roe deer fawn detection system. Int Arch Photogramm Remote Sens 38:1–5
Jouventin P (1982) Visual and vocal signals in penguins, their evolution and adaptive characters. Adv Ethol 24:148
Korczak-Abshire M, Kidawa A, Zmarz A, Storvold R, Karlsen SR, Rodzewicz M, Chwedorzewska K, Znój A (2016) Preliminary study on nesting Adélie penguins disturbance by unmanned aerial vehicles. CCAMLR Sci 23:1–16
Koski WR, Allen T, Ireland D, Buck G, Smith PR, Macrander AM, Halick MA, Rushing C, Sliwa DJ, McDonald TL (2009) Evaluation of an unmanned airborne system for monitoring marine mammals. Aquat Mamm 35:347
Kuznetsova A, Brockhoff PB, Christensen RHB (2015) Package 'lmerTest' R package version 2
Liu C-C, Chen Y-H, Wen H-L (2015) Supporting the annual international black-faced spoonbill census with a low-cost unmanned aerial vehicle. Ecol Inform 30:170–178. https://doi.org/10.1016/j.ecoinf.2015.10.008
Lucieer A, Robinson S, Turner D, Harwin S, Kelcey J (2012) Using a micro-UAV for ultra-high resolution multi-sensor observations of Antarctic moss beds. Int Arch Photogramm Remote Sens Spat Inf Sci. https://doi.org/10.5194/isprsarchives-XXXIX-B1-429-2012
McEvoy JF, Hall GP, McDonald PG (2016) Evaluation of unmanned aerial vehicle shape, flight path and camera type for waterfowl surveys: disturbance effects and species recognition. PeerJ 4:e1831. https://doi.org/10.7717/peerj.1831
McGill PR, Reisenbichler KR, Etchemendy SA, Dawe TC, Hobson BW (2011) Aerial surveys and tagging of free-drifting icebergs using an unmanned aerial vehicle (UAV). Deep Sea Res Part II 58:1318–1326. https://doi.org/10.1016/j.dsr2.2010.11.007
Mulero-Pázmány M, Jenni-Eiermann S, Strebel N, Sattler T, Negro JJ, Tablado Z (2017) Unmanned aircraft systems as a new source of disturbance for wildlife: a systematic review. PLoS ONE 12(6):e0178448
Müller-Schwarze D, Müller-Schwarze C (1977) Pinguine. Die Neue Brehm-Bücherei, Wittenberg Lutherstadt
Mustafa O, Esefeld J, Hertel F, Krietsch J, Peter H-U, Pfeifer C, Rümmler M-C, Staeding A, et al. (2014) Mapping of Pygoscelis penguins by using an UAV in the vicinity of southwestern King George Island. Paper presented at the XXXIII SCAR open science conference Auckland, New Zealand
Mustafa O, Esefeld J, Grämer H, Maercker J, Peter H-U, Rümmler M-C, Senf M, Pfeifer C (2017) Monitoring penguin colonies in the Antarctic using remote sensing data. On behalf of the German Environment Agency. Dessau-Roßlau. https://www.umweltbundesamt.de/publikationen/monitoring-penguin-colonies-in-the-antarctic-using
Peasgood S, Valentin M (2015) Drones: a rising market. An industry to lift your returns. Sophic capital
Pomeroy P, O'Connor L, Davies P (2015) Assessing use of and reaction to unmanned aerial systems in gray and harbor seals during breeding and molt in the UK. J Unmanned Veh Syst 3:102–113. https://doi.org/10.1139/juvs-2015-0013
R Development Core Team (2008) R: A language and environment for statistical computing R foundation for statistical computing
Ratcliffe N, Guihen D, Robst J, Crofts S, Stanworth A, Enderlein P (2015) A protocol for the aerial survey of penguin colonies using UAVs. J Unmanned Veh Syst 3:95–101. https://doi.org/10.1139/juvs-2015-0006
RStudio Team (2016). RStudio: integrated development for R. RStudio, Inc., Boston. http://www.rstudio.com/
Rümmler M-C, Mustafa O, Maercker J, Peter H-U, Esefeld J (2016) Measuring the influence of unmanned aerial vehicles on Adélie penguins. Pol Biol 39:1329–1334. https://doi.org/10.1007/s00300-015-1838-1
Schuster KC (2010) Impact of human and other disturbance on behaviour and heart rate of incubating Adélie penguins (*Pygoscelis adeliae*). Dissertation, Philips-Universität Marburg
Thomson RB (1977) Effects of human disturbance on an Adélie penguin rookery and measures of control. In: Llano GA (ed) Adaptations within Antarctic ecosystems. Smithsonian Institution, Washington, pp 1177–1180
Van Zinderen Bakker EM, Winterbottom JM, Dyer RA (1971) A behaviour analysis of the Gentoo penguin. In: Marion and Prince Edward Islands. Report on the south african biological and geological expedition/1965–1966. Balkema, Cape Town, p 251–272
Vas E et al (2015) Approaching birds with drones: first experiments and ethical guidelines. Biol Lett 11(2):20140754
Vermeulen C, Lejeune P, Lisein J, Sawadogo P, Bouché P (2013) Unmanned aerial survey of elephants. PLoS ONE 8:e54700. https://doi.org/10.1371/journal.pone.0054700
Weimerskirch H, Prudor A, Schull Q (2018) Flights of drones over sub-Antarctic seabirds show species-and status-specific behavioural and physiological responses. Pol Biol 41(2):259–266
Wilson RP, Coria NR, Spairani HJ, Adelung D, Culik B (1989) Human-induced behaviour in Adélie penguins *Pygoscelis adeliae*. Pol Biol 10:77–80