

RESEARCH ARTICLE

Variable effects of blade black-and-white designs on detection of turbine rotation by birds

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Abstract

1. Wind turbines can negatively impact biodiversity, particularly through bird collisions with blades. A common mitigation measure involves the rapid, temporary curtailment of turbines using automatic detection systems, though their effectiveness remains unproven. A passive alternative is to modify turbine appearance to improve visual detection by birds. Several visual factors—motion blur, limited sensitivity to achromatic contrasts and difficulty in detecting rotating blades—may influence their detectability by different species and, therefore, collision risk. Enhancing turbine detectability, by applying black-and-white patterns to blades, offers a promising pathway to reduce collisions. However, painting blades on existing turbines is costly and the monitoring needed to assess this technique's effectiveness can take several years. We aimed at determining which pattern(s) would be most effective in improving the detection of blade rotation by birds.
2. We used an experimental laboratory approach based on miniature wind turbines and operant conditioning, whereby captive-bred birds (black kites *Milvus migrans* and domestic homing pigeons *Columba livia*) were trained to respond to a positive visual stimulus with a food reward. The tests assessed the effect of four patterns—white blades, a black blade, striped blades and checkered blades—on the birds' detection of blade rotation.
3. We observed an effect of (1) the pattern, (2) the rotation speed of the blades and (3) the achromatic contrast between the blades and their background on the detection of blade motion by birds. More than 50% of tested individuals could not distinguish between stationary and slowly rotating turbines (<5 rotations per minute). Striped and checkered patterns improved blade motion detection in black kites, whereas a checkered pattern reduced motion detection in pigeons. High variability in rotation detection was observed both between and within species.

Constance Blary and Lucie Foucart are co-first authors.

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4. *Synthesis and applications.* Although no clear consensus emerged, striped patterns appeared to be the most promising for enhancing blade motion detection by several bird species. Field experiments are now required to validate these results in situ.

KEYWORDS

bird collision, blade rotation, motion detection, pattern design, sensory ecology, visual perception, wind turbines

1 | INTRODUCTION

At COP28 in 2023, nearly 200 countries committed to tripling renewable energy capacity and doubling energy efficiency by 2030. Wind energy was identified as a central, cost-effective solution to address climate change (IEA, 2024). While the development of wind power plants supports climate change mitigation efforts, it can negatively affect biodiversity (Wang & Wang, 2015), posing a 'green-green dilemma' between advancing the energy transition and conserving biodiversity (Dulluri & Raţ, 2019). Wind energy can impact biodiversity both directly, through collisions in the case of flying animals, and indirectly, through habitat loss or by acting as ecological barriers (Agudelo et al., 2021; Wang & Wang, 2015).

Currently, one of the solutions used to reduce mortality by collision at wind power plants is to stop or slow down the blades during high-risk periods. This can be done during extensive periods (e.g. nocturnal curtailment to protect bats; Whitby et al., 2024) or dynamically through the use of Automated Detection Systems (ADS) (Ballester et al., 2024). However, ADS are expensive, lead to production losses and their effectiveness in reducing mortality is poorly documented. To date, there has been only one international publication on the effectiveness of an ADS (McClure et al., 2022), which has been subsequently criticized (Huso & Dalthorp, 2023). It is therefore essential to explore alternative solutions to reduce bird mortality from wind turbines. One promising approach involves enhancing the visibility of wind turbines to birds. This idea was first proposed in the early 2000s based on studies of avian visual perception (Hodos, 2002; McIsaac, 2001), suggesting that limited blade detectability may increase collision risk. It was later supported by experimental work showing reduced bird collisions following increased blade contrast (May et al., 2020) and has recently gained further support from advances in avian visual ecology (e.g. Martin & Banks, 2023). To do so effectively, it is crucial to first understand how birds perceive these structures, as this knowledge can inform targeted mitigation strategies.

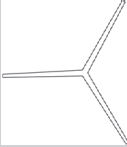
Despite the large size of wind turbines and the reduction of blade rotation speed by ADS when there is a risk, collisions still occur (Huso & Dalthorp, 2023). One of the visual factors that can explain this is the birds' failure to detect the motion of blades under certain conditions (Blary et al., 2023; Hodos, 2002; Martin & Banks, 2023). As an object increases in speed, animals may perceive motion blur, when an object tends to appear progressively blurrier to the observer (Pääkkönen & Morgan, 1994). Motion blur is influenced by

several factors, including the object's size and velocity, the distance between the object and the viewer and the viewer's ability to process rapidly changing visual information, referred to as temporal resolution (Hodos, 2002). While motion blur at high speeds seems evident, slow motion can also pose detection challenges. In humans, slow-moving objects are often perceived as moving even more slowly than they truly are (e.g. clouds in the sky); when below a certain speed threshold, they may even be perceived as stationary (Cavanagh et al., 1984). A similar effect has been reported in domestic doves (*Streptopelia roseogrisea*), which perceived miniature turbines rotating at less than 5 rotations per minute as stationary (Blary et al., 2023). This speed threshold is even higher when the achromatic contrast between the object and its background is lower, making detection more difficult (Blary et al., 2023).

One method to improve bird detection of wind turbines and increase their likelihood of detecting blade rotation is to enhance the achromatic contrast between the turbine and its background (Blary et al., 2023), as well as to distinguish the blades from each other (Hodos, 2002; Martin & Banks, 2023), through painting blades with black-and-white patterns. While this solution has shown some success, with May et al. (2020) finding a reduction in bird mortality when one blade was painted black at a wind power plant in Norway, its effectiveness appeared to be limited to a subset of species within the bird community (Klop et al., 2024; May et al., 2020). Other patterns than a single blade painted black are possible, but it is not easy to predict which will best improve the detection of wind turbines by birds, regardless of the rotating speed. Furthermore, it is likely that the best-performing pattern will vary among species, as their sensory organs have evolved differently and they may not perceive the world in the same way (see Martin (2017) for a review of bird visual abilities).

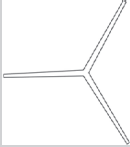
Another constraint is that painting the blades in situ on wind turbines that are already operational to test the effect of different patterns is expensive, and the upstream and downstream monitoring required to assess the effectiveness of each pattern could take several years (May et al., 2020). To get around this problem, we aimed to determine which pattern(s) would be most effective in improving the detection of blade rotation by birds with an experimental setup mimicking small wind turbines. We used this to test how birds perceive the slow rotation of turbines painted with four different patterns (Table 1), given that (i) pattern characteristics that limit motion blur have already been identified (Hodos, 2002), (ii) no characteristics have yet been identified that lower the threshold at which a rotating

TABLE 1 Blade pattern criteria that help birds detect wind turbines and blade rotation, the studies in which these were identified, and whether a criterion is met with the patterns used in our study.

Pattern name and description				
Criteria	Justification and method applied to respect the criterion	Pattern name and description		
		'white'	'black'	'striped'
1. The patterns must be detectable at great distances by as many species as possible	The ability of birds to detect small objects at long distances varies greatly between species (see Martin (2017) for a review of birds' visual abilities). Moreover, this ability depends on their achromatic contrast sensitivity. Birds are 7 to 30 times less sensitive to achromatic contrasts than humans (Blary et al., 2024). It is recommended to use large black-and-white patterns (Blary et al., 2023; Martin & Banks, 2023)			
		Three white blades	Two white blades and one black blade	Three striped blades, sited at non-overlapping distances to the blade tip
2. The patterns should limit the motion blur potentially perceived by the birds when the blades are rotating at high speed and/or enhance the flicker effect	Motion blur can be reduced by distinguishing the blades from one another, by varying or shifting the patterns between the blades (Hodos, 2002). Shifting the patterns between the blades may also increase flickering (Martin & Banks, 2023)	No	No (A single black blade does not increase contrast within the blade itself or between adjacent blades. Since blades are not visually contiguous during rotation, the contrast between them is not perceived as a unified signal)	Yes
		No	Yes	No
3. The patterns should improve the detection of blade rotation at low rotation speeds	Rotation detection can be improved by increasing the achromatic contrast between the blade and its background (Blary et al., 2023). As the background is highly variable, it is recommended to vary the achromatic contrast within each blade	No	No	Yes
4. The patterns must increase the rotation speed perceived by the birds	Increasing the speed perceived would limit the risk of birds crossing the rotor-swept area (Blary et al., 2025). Increasing contrast at the blade edges could enhance perceived speed, as shown in humans where motion is perceived faster when more contrast is available at the boundaries of a rotating object (Caplovitz & Tse, 2007)	No	No	Yes

(Continues)

TABLE 1 (Continued)

Criteria	Pattern name and description				Justification and method applied to respect the criterion
	'white'	'black'	'striped'	'checkered'	
5. The patterns must help birds predict the trajectory of the blades					As rotary motion is not commonly encountered in nature, birds may have difficulty predicting the trajectory of the blades, leading them to cross the area swept by the blades despite the risk of collision (Blary et al., 2025). Varying the density of the patterns on the blades may alter the perceived speed along different parts of the blade, thereby influencing the global motion perceived by the bird. Perceived motion arises from the integration of local motion cues (Adelson & Movshon, 1982; Bischof et al., 1999; Martinoya & Delius, 1990). In humans, Caplovitz and Tse (2007) have shown that increasing the density of visual markers on a rotating object enhances its perceived speed. Applying this principle, a higher pattern density near the hub and lower density near the tip could help reduce the perceived difference in speed along the blade, making the overall motion appear more uniform, closer to translational movement
	Three white blades	Two white blades and one black blade	Three striped blades, sited at non-overlapping distances to the blade tip	Three blades painted with checks, with increase in density of checks towards the centre of the turbine	
	No	No	No	Yes	

object would be perceived as stationary by birds (Blary et al., 2023), (iii) the effect of different patterns at high rotation speeds has already been evaluated on kestrels (Hodos, 2002) and (iv) the decision to cross the rotor-swept area is more likely at low rather than high rotation speeds (Blary et al., 2025). The ability to detect slow-rotating blades was tested in two bird species with different ecologies: rock doves (domestic variety; aka homing pigeon, *Columba livia*) and black kites (*Milvus migrans*). The experiment used operant conditioning on captive birds, following the same procedure as Blary et al. (2023).

In order to increase the detectability of wind turbines and blade rotation by birds, as many as possible of the criteria listed in Table 1 must be met: the pattern must be detectable at a great distance, limit motion blur and/or enhance the flicker effect (Hodos, 2002; Martin & Banks, 2023), improve the detection of blade rotation, increase the rotation speed perceived and help birds predict the trajectory of the blades. Based on this, we tested four patterns in this study (Table 1): (1) three white blades ('white'), (2) two white blades and one black blade ('black'), (3) three striped blades ('striped') and (4) three checkered blades ('checkered').

We predicted that (i) the ability of birds to detect rotating blades would vary depending on the visual pattern of the blades, their achromatic contrast with the background and the rotation speed. We also predicted that (2) birds would be less able to detect rotation at lower speeds and with uniformly white blades. Finally, we predicted (3) that birds' ability to detect turbine rotation would differ between light and dark backgrounds with the white blades, due to the marked contrast shift. A similar effect may also occur with the single black blade ('black'), as the contrast change affected only one blade. We thus expected 'striped' and 'checkered' to be the most effective patterns in helping birds detect blade rotation, regardless of rotation speed or background conditions.

2 | MATERIALS AND METHODS

2.1 | Study sites and experimental subjects

The current manuscript's methods are based on the methods described in Blary et al. (2023). The experiment was carried out at two locations in France where the study birds were housed: the Centre of Functional and Evolutionary Ecology (CEFE) in Montpellier and the falconry of Puy du Fou France (hereafter, PdF) in Les Epesses. The study was carried out in parallel with 15 healthy adult birds: from February to August 2024 with 8 rock doves (domestic variety; aka homing pigeons; hereafter 'pigeons') housed at the CEFE, and from March to June 2024, with 7 black kites (hereafter 'kites') housed at the PdF. The birds were kept in outdoor aviaries with permanent access to water. The pigeons were fed 20 g of seed each day (Prestige Doves, Versele Laga), while the kites were fed with chicken meat to maintain them at 90% of their usual body weight. On experimental days (5 to 7 days a week), the birds were fed only during the experiment. On non-experimental days, food was distributed in the aviaries in the morning only.

Due to multiple constraints, we selected two bird species with contrasting ecologies and visual capacities to explore potential interspecific differences. (1) Logistical constraints: the number of species was limited by the time-intensive nature of the experiments; only 6–8 individuals could be trained per day, requiring daily handling over several months. The CEFE could host only one domestic species, while the PdF had numerous black kites in its captive collection. (2) Captive availability: the study required daily, stress-free handling, which restricted us to captive individuals. Species selection was therefore dependent on those available at the two sites. Given their high collision risk and availability at the PdF, we chose a raptor species susceptible to collision mortality. (3) Existing knowledge: to ensure robust experimental conditions and interpretation of the results, we selected species for which sufficient data on visual capacities were available (at least achromatic contrast sensitivity function). Pigeons are widely studied, easy to train and allow comparison with Blary et al. (2023); while not of conservation concern, they are occasionally involved in turbine collisions. Black kites are easy to train, with sufficient data on their visual system and are also frequently affected by collisions, especially the closely related red kite *Milvus milvus*, of conservation concern in Europe (Santos et al., 2021; Schaub, 2012; Schaub et al., 2024). Note that we performed similar experiments at PdF with another species, the Griffon vulture *Gyps fulvus*, which is highly impacted by wind turbine collisions (De Lucas et al., 2008; Sassi et al., 2024; Sebastián-González et al., 2018). We tried to train 6 individuals with the same procedure as black kite (see below). However, only one individual could be efficiently conditioned. Therefore, the adjustments in methods required for the vulture and the results are presented in Supporting Information A.

2.2 | Ethics statement

The experiments were conducted in accordance with the European Union directive on the protection of animals used for scientific purposes (2010/63/EU) and French legislation. The protocol and species studied were approved by a local French ethics committee for animal experimentation and authorized by the French Directorate General for Research and Innovation (APAFIS#31775–2021041311196892 v5). In compliance with French law, the kites (and vultures) were handled by their regular trainers under the PdF's permit (national certificate to maintain birds 17–85–154). At the end of the experiment, all individuals remained at the PdF in their usual conditions. The pigeons are owned by breeder Andrée Chardon, who kindly lent them for the duration of the study. All pigeons were returned to the owner at the end of the experiment.

2.3 | Blade pattern design

To be effective in reducing bird collision with wind turbines, patterns must meet as many as possible of the criteria listed in

Table 1 (be detectable at a great distance, limit motion blur and/or enhance the flicker effect; Hodos, 2002; Martin & Banks, 2023, improve the detection of blade rotation, increase the rotation speed perceived and help birds predict the trajectory of the blades). Four patterns were tested (**Table 1**): (1) three white blades ('white'), (2) two white blades and one black blade ('black'), (3) three striped blades ('striped') and (4) three checkered blades ('checkered').

The 'white' pattern was used as a control as it does not meet any of the listed criteria (**Table 1**), but represents the current appearance of wind turbines. The 'black' pattern corresponds to the one successfully tested by May et al. (2020); it meets only one criterion, as it was designed with the specific aim of limiting the motion blur potentially perceived by birds (Hodos, 2002; May et al., 2020) (**Table 1**). The 'striped' pattern meets the first four criteria (**Table 1**). The 'checkered' pattern meets criteria 2, 3 and 4, and attempts to meet criterion 5, to the detriment of criterion 1 (smaller patterns) (**Table 1**). In this pattern, the spacing between the squares progressively increases from the blade base to the tip. The aim is to compensate for the natural increase in linear speed along the blade: a higher density of squares near the hub and lower density near the tip are intended to reduce the variation in perceived speed, making the rotation to appear more uniform, as if the blade was translating rather than rotating. This design was based on studies showing that global motion perception depends on the integration of local motion cues (Adelson & Movshon, 1982; Bischof et al., 1999; Martinoya & Delius, 1990) and that increasing the density of visual marker can enhance perceived speed in rotating objects (Caplovitz & Tse, 2007). However, in the present study, we did not aim to assess whether this pattern alters perceived speed. Investigating this question would require dedicated perceptual studies. Here, the aim was to focus on a more fundamental aspect: whether the pattern improves birds' ability to detect that the blades are rotating, which is a prerequisite for initiating avoidance behaviour of wind turbine rotating area.

In the 'striped' pattern, the 6.5-cm stripes were separated by 13 cm (**Figure S1**). In the 'checkered' pattern, the 4-cm² squares were separated by 1 cm in the inner third of the blades, by 2 cm in the second third and by 3 cm in the outer third (**Figure S1**). For both 'striped' and 'checkered', the positions of the stripes or squares shifted from one blade to another, so that no pattern elements overlapped between blades (**Figure S1**). The dimensions of the patterns were determined based on the birds' contrast sensitivity function (Blary et al., 2024), taking into account the size of the small turbines used in the experiment and the distance between the birds and the turbines (see Supporting Information **Equation S1** for details on the formula used). The dimensions of the stripes were selected to ensure maximum detectability by the species tested. For the checkered patterns, dimensions were calculated to be small enough to allow variation in pattern density across the blades, yet large enough to remain detectable by the birds used in the experiment. See **Figure S1** for detailed dimensions.

2.4 | Experimental design

2.4.1 | Experimental area

For each study site, eight miniature wind turbines (hereafter 'turbines') were designed for the experiment: two turbines for each pattern (**Figure 1**). The blades were made of 10-mm thick white PVC (Celuka expanded PVC, Prolians). Their proportions corresponded to those of real wind turbines, with a turbine diameter of 160 cm, a blade width varying from 7 cm at the base to 2 cm at the tip and a hub diameter of 7 cm. The visual configuration experienced by the birds was equivalent to viewing a real 100-meter-diameter wind turbine from a distance of approximately 190 m. The blades and hub were attached to a horizontal rod connected to an electric motor (SD1-4.2A-21, IMO Precision Controls) that allowed the turbines to rotate clockwise or counterclockwise (to control for any potential bias due to individual differences in the perception of rotation direction), between 0.5 and 30 rotations per minute (rpm). The rotational speed of these turbines was measured using a triaxial accelerometer (Axytrek, Technosmart) based on the method used by Blary et al. (2023). The justification for the rotation speeds used in this study is detailed later in the Section 2.4.2.

The experiment with kites (and vultures, see **Supporting Information A**) at the PdF falconry took place in an outdoor aviary. Because of outdoor conditions, illuminance at the location of a bird's head was measured with a light meter before each experiment: average 244.0 ± 9.8 lux [mean $\pm$ SE] (Hagner ScreenMaster, B. Hagner). Opaque wooden fences 1.80-m high were placed around the experimental arena to limit undesirable external visual stimuli (**Figure 1**). The kites were placed in a wooden box facing two turbines (20 $\times$ 100 $\times$ 60 cm; depth $\times$ width $\times$ height), located 400 cm from the birds. Turbines were placed behind a 200 $\times$ 200 cm plexiglass panel, 10-mm thick (PVC Celuka, Prolians). In this way, birds could not collide with the turbines or the motors used to turn them, eliminating the risk of injury. The kites' box was placed high enough to ensure that the birds' eyes were at the same height as the turbine hubs during the experiments. Two perches connected to food dispensers were placed on either side of the two turbines at the hub height (**Figure 1a,b**).

The experiment conducted with the pigeons at the CEFE took place in a 6 $\times$ 6-m² greenhouse, the walls, floor and ceiling of which were covered with white fabric (Svensson Harmony 5747 FR) to block all undesirable external visual stimuli, but allowing natural light to pass through. Neon lights (Ledeven L100.600.11.120.1; 60 Hz, 90 W) on the ceiling were adjusted to maintain a stable light level of over 4000 lux throughout the day (7339 ± 42 lux [mean $\pm$ SE], measured at the bird's head with a lux meter before each experiment; Hagner ScreenMaster, B. Hagner). The experimental setup was similar to that used for the kites, with an identical layout and dimensions to the experimental setup used by Blary et al. (2023) for Harris's hawks (*Parabuteo unicinctus*). Pigeons were placed in a wooden box (28.5 $\times$ 25.5 $\times$ 25.5 cm) located 1 m above ground and 3 m from the turbines.

For each species studied, the background behind the turbines could be modified to dark grey (Michelson contrast of 0.75 between

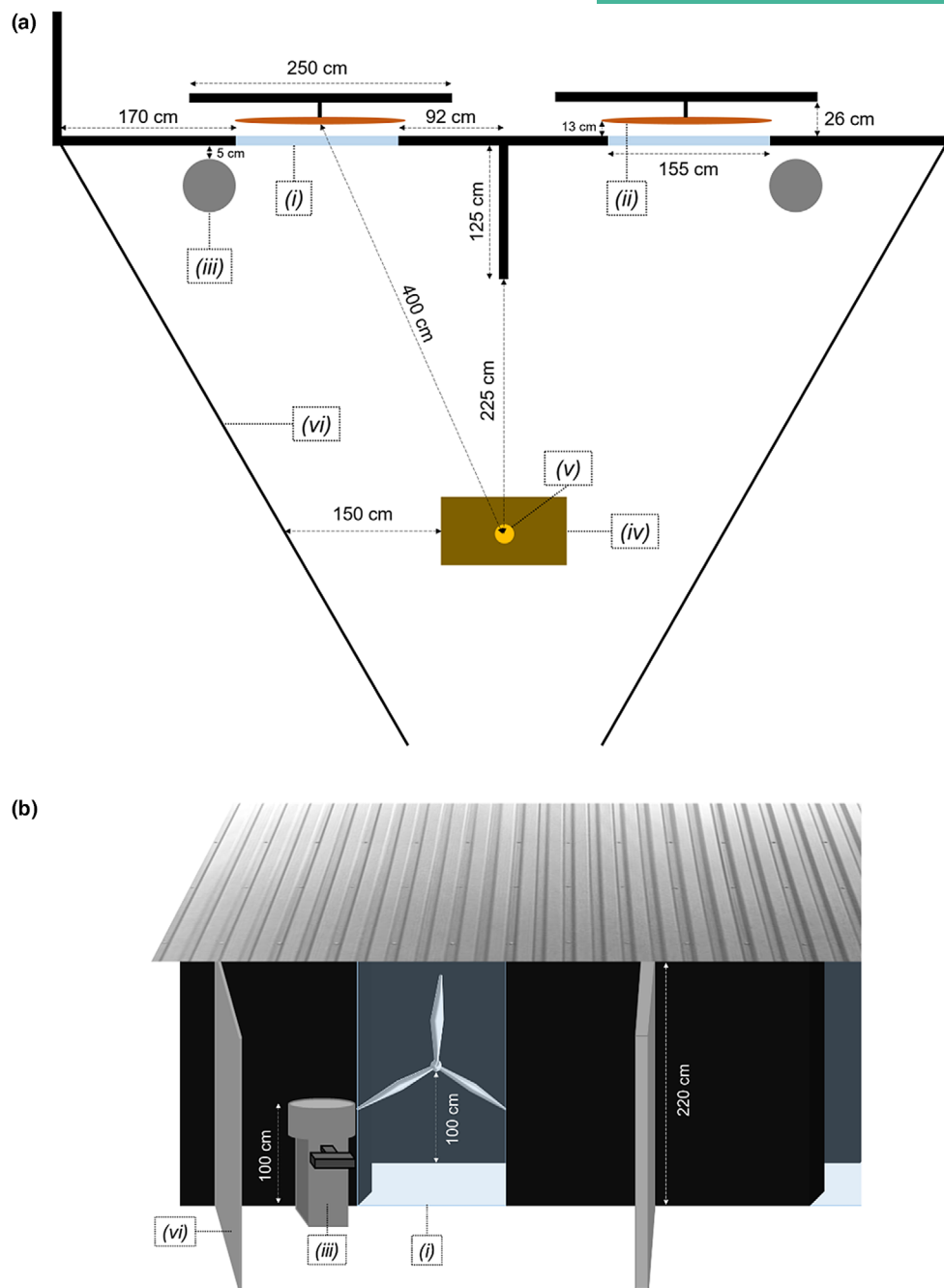


FIGURE 1 Experimental setup used for black kites (*Milvus migrans*), seen from above in 2D (a) and from the front in 3D (b). The setup includes Plexiglas panels (i) in front of the two turbines (ii), perches on either side of the turbines (iii) and a starting box (iv), as well as the position of the kites' heads when they are placed in the box (v). Opaque fences (vi) were placed around the experimental arena to limit any undesirable visual stimuli.

the white parts of the turbine and the background and a contrast of 0.25 with the black parts) or light grey (Michelson contrast of 0.25 between the white parts of the turbine and the background and a contrast of 0.75 with the black parts; measured with a luxmeter, Hagner Screen-Master, B. Hagner, Sweden).

2.4.2 | Experimental procedure

We performed operant conditioning on the birds, including a conditioning phase and a testing phase. Birds were trained to

discriminate between two visual stimuli placed side by side: a stationary turbine, consistently associated with a food reward (positive stimulus) and a rotating turbine, which was not rewarded (negative stimulus). Our procedure followed the general approach described in Blary et al. (2023), with the main differences being the use of multiple blade patterns, against specific backgrounds and the rotation speeds. The conditioning phase was carried out with the dark grey background only, at 10 and 20 rpm, representing the most commonly encountered lower and higher rotation speeds of real wind turbines (Khalfallah & Koliub, 2007). Two patterns were used to avoid habituation, limit the number of patterns for protocol

simplicity and minimize interference during learning. The patterns 'black' and 'white' were selected, with 'black' chosen based on its proven effectiveness for training (Blary et al., 2023) and 'white' as the most visually similar alternative. The test phase was carried out with the four patterns and the two dark and light grey backgrounds, at 1, 5, 10 and 20 rpm, with 1 and 5 rpm reflecting the speed range reached by the blades when ADS triggers a slowdown (Fluhr et al., 2025).

To prevent pigeons from being influenced by the noise produced by the rotation (52 ± 1 dB [mean $\pm$ SE]; measured with the Décibel X—dB Sonomètre application on a smartphone at the bird's head), a white noise corresponding to engine noise was broadcasted (58 dB). For the kites, due to the setup configuration (with turbine motors placed inside a closed room and experiments conducted outdoors in a theme park with concurrent public shows and background music), ambient noise at the birds' location consistently exceeded the sound produced by the motors (no differences in dB sound level whether the turbines were rotating or not, or whether white noise was present or not). As a result, no additional ambient noise was introduced. This acoustic environment did not pose any issues for the birds, as the kites had been living at the PdF falconry since birth and were habituated to such sounds. Therefore, we assumed that they did not interfere with the experiment.

Conditioning phase

Each individual was trained once a day, 5 to 7 days a week, with one to two training sessions per day. The daily training sessions consisted of 16 trials for the pigeons and 32 trials for the raptors (the latter being able to ingest twice as much food reward compared to pigeons). Thus, for each session, the negative stimulus (rotating turbine) was presented eight times (four in each direction of rotation: two at 10 rpm and two at 20 rpm) on each side (the left or right of the pair of turbines) for pigeons and 16 times (eight in each direction of rotation: four at 10 rpm and four at 20 rpm) for kites. The blade patterns were changed randomly between each session, alternating 'white' with 'black'. A single pattern was used within a single session.

Between each trial, the bird was returned to the closed wooden box to prevent it from seeing the change in stimulus (switching the rotating turbine to the left side or right side and changing the speed). Pigeons and kites were gently returned to the box by the experimenter, without restraining them. Once the stimulus was modified, the box was opened to allow the bird to see both turbines and decide where to go. The experimenter, hidden behind the bird's starting box, could trigger the food distribution remotely, providing an immediate reward if the bird chose the correct stationary turbine.

When a bird reached 75% correct choices in four consecutive sessions for pigeons and 80% correct choices in two consecutive sessions for kites (and vultures), we ended the conditioning phase and began the testing phase. These thresholds ensured that the bird's choices were not random (binomial test with $p < 0.05$ at each session and a total of 64 trials per bird).

Testing phase

One or two testing sessions per day were carried out with each individual, with 16 trials per session for pigeons and 32 trials for kites (and vultures). To ensure that the birds were still conditioned, each session began with four training trials (with the negative stimulus rotating at 10 or 20 rpm), one on each side (left or right) and in each direction of rotation. These four trials were not included in the results.

Each speed tested (1, 5, 10 and 20 rpm) was presented an equivalent number of times and in a pseudo-random order during each session. We did not include 3 rpm, as tested in Blary et al. (2023), because they found no effect for Harris's hawks at this speed, likely due to a detection threshold being too high. Since wind turbines can rotate as slowly as 1 rpm during ADS-triggered slowdowns, we aimed to test rotation detection at 1 rpm to avoid missing potential effects. We selected 5 rpm to evaluate the influence of achromatic contrast between blade and background, which may not be detectable at lower speeds (Blary et al., 2023). A single blade pattern and background were used within each session, but patterns and backgrounds were changed randomly between sessions. Each combination of speed, pattern and background was presented 32 times to each individual (16 times on each side, eight times clockwise and eight times counterclockwise).

2.4.3 | Analyses

All statistical analyses were performed with R (v. 4.2.3). Mean values are presented with their standard error ($\pm$). We conducted two complementary analyses to assess both the birds' ability to detect blade rotation and the factors influencing the accuracy of their responses.

The first analysis aimed to determine the minimal conditions under which rotation was detected. For this purpose, we performed binomial tests for each individual and each combination of speed $\times$ pattern $\times$ background tested, using a statistical significance threshold of $p = 0.05$ and a Bonferroni correction for multiple comparison.

The second analysis focused on how visual variables (speed, pattern, contrast) affected the probability of correct detection. We used binomial GLMMs (glmmTMB package v1.0.2.1; Brooks et al., 2017) to assess the effect of (1) rotation speed, (2) blade patterns and (3) background (i.e. high or low contrast with the white parts of the turbines) on the birds' ability to distinguish the stationary from the rotating turbine. We first fitted a model containing the three fixed effects (pattern, speed and background) with three-way interactions, and including the date of the session and the identity of the individual as a random effect to account for repeated measures and temporal variability (one model per species). Model simplification was then performed using a stepwise backward likelihood-based approach. Specifically, interaction terms were sequentially removed starting from the highest-order interaction, and nested models were compared using likelihood ratio tests. At each step, the significance of the removed term was assessed by comparing the reduced model to the more complex model. Non-significant

interaction terms ($p > 0.05$) were excluded, while significant terms were retained. This procedure was repeated iteratively until further simplification resulted in a significant loss of model fit. The same model selection procedure was applied independently to the pigeon and kite datasets.

When the selected model included interaction terms, post hoc analyses were conducted using estimated marginal means to facilitate interpretation of the interactions. Those post hoc analyses were computed for the pattern conditional on combinations of speed and background. Predicted values were evaluated at the observed speed values (1, 5, 10 and 20 rpm). Pairwise comparisons among patterns were then performed with Bonferroni correction for multiple testing. When the selected model did not include interaction terms, estimated marginal means for patterns were calculated and pairwise comparisons among patterns were conducted using Bonferroni-adjusted tests. All post hoc analyses were performed on the final selected models using the emmeans package (v1.6.0).

3 | RESULTS

We successfully trained six out of eight pigeons, five out of seven kites (and one out of six vultures, see [Supporting Information A](#)). Pigeon training required between 42 and 67 sessions, while training raptors was much faster (5–19 sessions for kites). The data were collected with both light and dark grey backgrounds for the six pigeons and five kites.

3.1 | Threshold of blade rotation detection across speeds, patterns and contrasts

With the dark grey background, all pigeons and kites were able to discriminate the stationary from the rotating turbine at speeds of 5, 10 or 20 rpm, irrespective of the blade pattern ([Figure 2](#)). However, at 1 rpm, at least four out of five pigeons failed to discriminate between the two turbines, regardless of the pattern ([Figure 2](#)). Of the kites, at 1 rpm, two out of five individuals failed to discriminate the stationary from the rotating turbine with 'white', and three individuals failed with 'black' ([Figure 2a,b](#)), while all succeeded with 'striped' and 'checkered' ([Figure 2c,d](#)).

With the light grey background, all pigeons and kites tested were able to discriminate the stationary turbine from the rotating turbine at speeds of 5, 10 or 20 rpm, whatever the pattern ([Figure S2](#)), with the exception of two pigeons at 5 rpm with 'checkered' ([Figure S2D](#)). At 1 rpm, two pigeons failed to discriminate the stationary from the rotating turbine with 'white' ([Figure S2A](#)), while with 'black', 'striped' and 'checkered', $\geq 65\%$ were unable to perform this task ([Figure S2B–D](#)). Of the kites, four individuals were unable to discriminate the stationary from the rotating turbine with 'white' at 1 rpm ([Figure S2A](#)), and two were unsuccessful with 'black' at the same speed ([Figure S2B](#)). All kites succeeded at 1 rpm with 'striped' and 'checkered' ([Figure S2B–D](#)).

3.2 | Impact of speed, pattern and contrast on the probability of blade rotation detection

The final selected model for pigeons retained two-way interactions between speed and background, and between speed and pattern, as their inclusion significantly improved model fit according to likelihood ratio tests ([Tables SM.B1](#) and [SM.B2](#)). The probability of pigeons to discriminate a stationary from a rotating turbine was higher at high speed ($p < 0.001$; [Figure 3a,b](#), [Table SM.B3](#)). For both backgrounds, the probability of pigeons to discriminate a stationary from a rotating turbine varied with pattern, particularly at low speeds ([Figure 4](#); [Table SM.B4](#)). At 1 and 5 rpm, the lower discrimination accuracy was observed for the 'checkered' pattern, while others were similar ([Table SM.B4](#)). Indeed, at 1 rpm individuals were 1.7 and 1.4 times more likely to succeed with 'white' ($p = 0.001$) or 'black' ($p = 0.04$) than with 'checkered', respectively ([Table SM.B4](#)). At 5 rpm, success probability was 1.5 and 1.4 times higher with 'white' ($p = 0.002$) and 'stripes' ($p = 0.01$) than with 'checkered', respectively ([Table SM.B4](#)). At 10 rpm, individuals were 1.4 times more likely to succeed with 'stripes' than with 'checkered' ($p = 0.04$) ([Table SM.B4](#)).

For kites, the model without interactions provided a better fit than models with interactions, as indicated by the likelihood ratio test ([Tables SM.C1](#) and [SM.C2](#)). Similarly to pigeons, the probability of kites to discriminate a stationary from a rotating turbine was higher at high speed ($p < 0.001$) and with a dark grey background than with a light grey background ($p = 0.03$; [Figure 3c,d](#); [Table SM.C3](#)). Regardless of rotation speed, the highest discrimination accuracy was observed for the 'stripe' and 'checkered' patterns. Individuals were, respectively, 1.8 and 1.7 times more likely to succeed with 'stripes' ($p = 0.002$) and 'checkered' ($p = 0.01$) than with 'white' ([Table SM.C4](#)). They were also 1.7 times more likely to succeed with 'stripes' than with 'black' ($p = 0.01$) and tended to succeed 1.6 times more with 'checkered' than with 'black' ($p = 0.06$; [Table SM.C4](#)).

4 | DISCUSSION

To our knowledge, this study is the first behavioural experiment to test how different achromatic patterns affect blade rotation perception in several bird species. We found that none of the individuals studied were able to consistently detect turbine rotation across all conditions; each failed in at least one combination of rotation speed, blade pattern, or background contrast. As suggested by Blary et al. (2023), low rotational speeds may lead to collisions, as the blades could be perceived as stationary by birds. We found that applying certain black-and-white patterns to the turbine blades could increase the likelihood of birds detecting the rotation of the blades at low speeds, but there was great variability depending on the pattern and the species. While birds were trained only on the 'white' and 'black' patterns, this partial training may have biased the results. However, control trials at 10 and 20 rpm showed similar performance across all patterns, indicating that the observed differences at lower

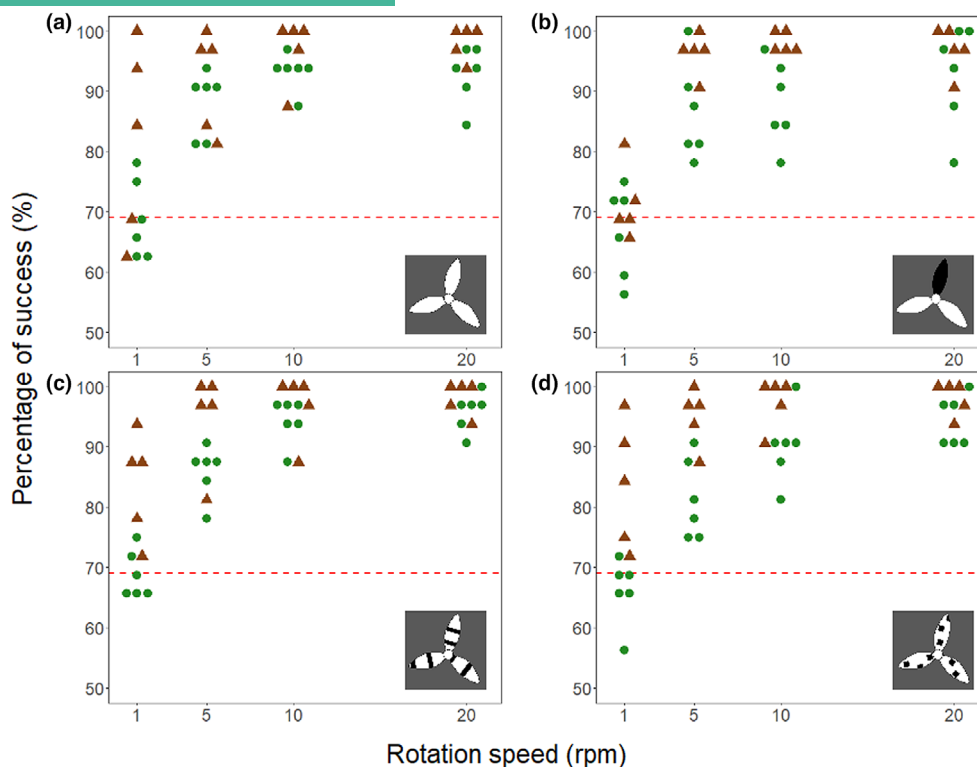


FIGURE 2 Percentage of bird success in discriminating a stationary from a rotating turbine as a function of rotation speed for domestic pigeons (*Columba livia domestica*; green circle) and black kites (*Milvus migrans*; brown triangle) against a dark grey background with three white blades (a, pattern 'white'), two white blades and one black blade (b, pattern 'black'), three striped blades (c, pattern 'striped'), or three checkered blades (d, pattern 'checkered'). The dotted red line represents the detection threshold (binomial test, $p < 0.05$): All points below this line indicate a combination of pattern $\times$ speed where the birds failed to discriminate between the stationary and rotating turbines.

speeds are attributable to the visual properties of the patterns rather than prior familiarity. These findings indicate that caution is needed when selecting patterns intended for application on wind turbines, as visual effectiveness varies between species. Some patterns may even reduce detectability compared to unmarked blades for certain species, underlining the importance of species-specific considerations. The pattern that nevertheless appeared to be the most effective in preventing birds from perceiving turbines as stationary was the striped pattern. This pattern increased the likelihood that black kites would detect rotating blades at low speeds, without altering this probability for pigeons (unlike checkered blades, which decreased it). The anecdotal results from the griffon vulture also highlight the striped pattern as most efficient to increase detection at reduced rotation speed (Supporting Information A).

Our results for pigeons were consistent with those of Blary et al. (2023) with domestic doves, showing a rotating speed threshold between 1 and 5 rpm below which the birds were unable to detect rotation when the achromatic contrast between the turbine and the background was high. We also found that rotation speed affected rotation perception in the raptors tested. The inability of the studied species to distinguish a turbine rotating at 1 rpm from a stationary one suggests that low rotation speeds may be inherently imperceptible to most bird species, preventing them from recognizing the movement as a potential threat. The achromatic

contrast between the blades and the background also proved to be an important parameter in birds' rotary motion detection, with lower contrast reducing the probability of detecting rotation by birds. However, this effect was less pronounced than in Blary et al. (2023), which found a clear difference between high and low contrast conditions at 5 rpm, with birds failing to detect rotation at low contrast. We found no such difference at that speed in our experiment. This may be due to a difference in rotation detection threshold between species and the absence of a test at an intermediate speed between 1 and 5 rpm, for which we may have observed a significant difference in birds' ability to detect rotation between the dark grey and light grey backgrounds.

Our results also revealed high variability in rotation detection in kites and pigeons. One might consider that the observed differences between species arose from differences in luminosity, which was relatively high and stable in pigeons, but lower and more variable in kites. However, this factor was accounted for in the statistical models through the inclusion of days as an explanatory variable. Additionally, perceived rotation speed is known to be negatively correlated with luminosity only at high speeds, with no impact of luminosity at low rotation speeds (Vaziri-Pashkam & Cavanagh, 2008). Because our observations concerned low speeds, this effect is unlikely to fully explain the differences observed between species. The variability observed in rotation detection was especially high for the 'white' and

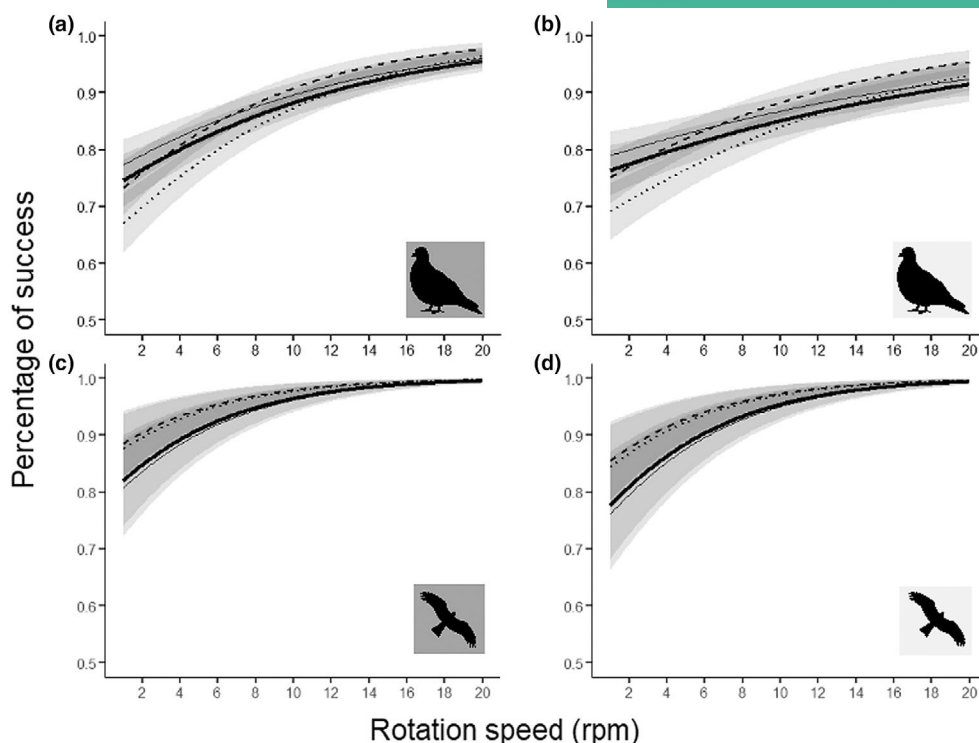


FIGURE 3 Prediction of the percentage of success in discriminating a stationary from a rotating turbine of domestic pigeons (*Columba livia domestica*) (a and b) and black kites (*Milvus migrans*) (c and d) as a function of rotation speed and blade pattern: Three white blades ('white')—thin line; two white blades and one black blade ('black')—thick line; three striped blades ('striped')—thick dotted line; three checkered blades ('checkered')—thin dotted line, when the background is dark grey (a and c) or light grey (b and d). Predictions are based on binomial GLMMs, with the speed and the background, as well as the speed and the pattern in interaction for pigeons, without interactions for kites. The 95% confidence interval for each pattern is indicated by a light grey zone around each curve.

'black' patterns in black kites, and for the 'white', 'black' and 'checkered' patterns in pigeons. In contrast, the 'striped' pattern, with broad elements on all blades and high-contrast leading edges, appeared more effective at minimizing perceptual variability across individuals at low rotation speeds. This suggests that such a striped pattern may be better suited to account for species and individual-level differences in visual sensitivity, increasing the likelihood that all birds can detect the blade pattern and perceive that the blades are rotating.

As predicted, given the highly contrasting patterns on each blade, 'striped' and 'checkered' most increased the likelihood of birds detecting blade rotation, but only for black kites (and the vulture). This prediction did not hold for 'checkered' pattern for pigeons. This may be linked to the inability of pigeons to detect the squares on the blades. Studies have shown that birds are able to detect a black square on a white background at a greater distance if the object is stationary than if it is moving (Haller et al., 2014; McIsaac, 2001). It is thus likely that, as the object rotated, the pigeons were no longer able to distinguish the black-and-white squares on the checkered blade. The pattern may have appeared as a uniform grey, resulting in a lower overall luminance perceived by the bird compared to the white part of the blade. Consequently, the luminance difference between the blade and the dark background would be reduced from the pigeon's perspective, decreasing the bird's probability of detecting the rotation.

Since a wide variety of species are affected by collisions (Thaxter et al., 2017), all of which differ in visual ability, and as birds need to detect both wind turbines and whether they are rotating from the longest achievable distance, large patterns should be favoured, such as the 'striped' pattern tested in this study. Although the striped pattern did not affect the speed threshold at which pigeons perceived the blades as stationary (compared to the control all-white blades), painting the blades with stripes would still be an effective solution for increasing the distance at which the birds could detect the turbines, as this pattern increases the achromatic contrast both on a blade itself and between the blades and the background (Blary et al., 2024).

Spatial resolution and contrast sensitivity are key factors influencing the detection of objects at a distance. Certain species (such as black kites) possess high spatial resolution (Potier et al., 2016) and relatively good achromatic contrast sensitivity compared to other bird species (Blary et al., 2024), enabling them to detect fine, high-contrast patterns at great distances. However, other species, like the house sparrow (*Passer domesticus*), have lower spatial resolution (Dolan & Fernández-Juricic, 2010) and poorer achromatic contrast sensitivity (Blary et al., 2024), limiting their ability to perceive the same patterns at equivalent distances (see Blary et al., 2024; Martin, 2017, for respective reviews on birds' visual acuity and achromatic contrast sensitivity). Designing large, high-contrast blade

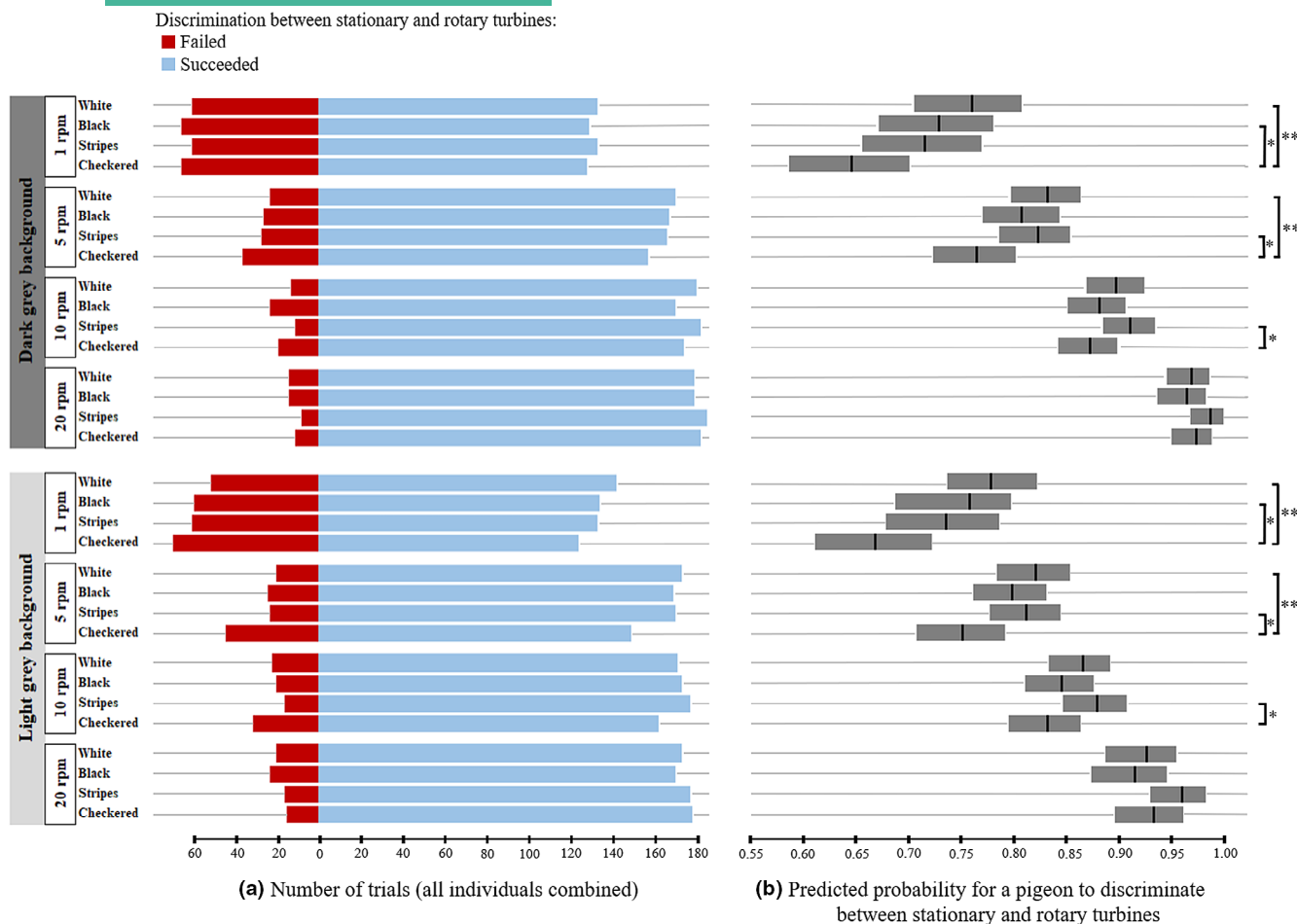


FIGURE 4 (a) Number of trials in which domestic pigeons (*Columba livia domestica*) succeeded (blue) or failed (red) to discriminate between a stationary and a rotating turbine, depending on the background, rotation speed and pattern. (b) Predicted probability of a pigeon successfully discriminating between a stationary and a rotating turbine, as a function of background, rotation speed and pattern, based on a binomial GLMM (black lines represent the mean prediction; grey shaded areas indicate the 95% confidence interval).

patterns could increase visibility across species with varying visual capacities.

One explanation for the variation in blade-speed perception could be temporal resolution, which affects the ability to perceive rapid changes in the visual environment (Donner, 2021). This capacity, linked to the number of distinct visual frames processed per second by the retina, varies highly between birds (see Donner, 2021, for a review) and is particularly relevant for detecting the rotation of wind turbine blades. Birds with high temporal resolution can detect fast-moving objects more effectively, as they can process visual information at a higher rate (Donner, 2021), but little is known about the relationship between this capacity and the visual detection of slow-moving objects. If an individual possesses high temporal resolution, it can be hypothesized that when a turbine rotates slowly, successive frames may appear very similar, potentially giving the impression that the blades are stationary. However, data on temporal resolution and movement detection across different species are currently limited, making it challenging to assess its impact comprehensively. In addition, evidence suggests there is a trade-off

between spatial and temporal resolution in vertebrates, requiring individuals to balance spatial resolution with temporal resolution over time (Donner, 2021). Further research is needed to evaluate the role of temporal resolution in relation to spatial resolution in the visual detection of moving objects such as wind turbine blades. Further studies will also be necessary to investigate the perceptual and neural mechanisms underlying birds' responses to rotating patterns; in order to better understand how such visual cues are processed and ultimately lead to (un)detection.

In any case, the results of our experimental study indicate that painting blades with black-and-white patterns is a promising solution to decrease bird mortality at wind power plants, potentially more effective than using a single black blade, as tested at wind turbine sites in Norway and the Netherlands (Kleyheeg-Hartman et al., 2025; May et al., 2020), with additional unpublished results from other sites presented at the 2025 Conference on Wind Energy and Wildlife. Turbine masts should also be painted to maximize effectiveness of the pattern (i.e. increasing the flickering effect; Martin & Banks, 2023), but also because collisions with

the mast itself also pose a significant risk (Stokke et al., 2020). Combining black-and-white patterns on wind turbines with ADS should equally be considered, as this approach could provide the most effective means of preventing collisions. In situ testing, including radar-based ornithological monitoring rather than focusing solely on mortality, for instance, will be essential to understand the real effect of black-and-white patterns on birds' avoidance behaviour of wind turbines.

A potentially negative effect of using visual patterns on wind turbines to enhance bird detection must also be considered: detectable from a greater distance, they could lead to increased habitat avoidance and larger areas of displaced birds. Beyond ecological concerns, the social acceptability of highly visible blade patterns should be explored, conducting surveys to gauge public perception. Raising awareness about the potential conflict between wind energy development and biodiversity, and how visual modifications can mitigate bird mortality, will be crucial to win broad support and the long-term success of these mitigation measures.

AUTHOR CONTRIBUTIONS

Aurélien Besnard, Olivier Duriez and Constance Blary secured funding and designed the project. Thierry Bouchet enabled the study by granting access to Puy du Fou birds and contributing his avian expertise. Simon Potier contributed to the study design, data analysis and interpretation. Claire Million-Ranquin, Laurant Laval, Lucie Foucart and Constance Blary conducted the experiments. Lucie Foucart and Constance Blary analysed the data and co-wrote the manuscript. All authors reviewed and edited the final version of the article.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data supporting the findings of this study are provided in Dryad: <https://doi.org/10.5061/dryad.kpr4xhm3> (Blary et al., 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure SM.A1. Experimental setup used griffon vultures (*Gyps fulvus*) seen from above in 2D. The setup includes Plexiglas panels (i) in front of the two turbines (ii), iron box on either side of the turbines (iii), a log (vi) and a starting box (v). Opaque fences (vi) were placed around the experimental arena to limit any undesirable visual stimuli.

Figure SM.A2. Percentage of success in discriminating a stationary from a rotating turbine as a function of rotation speed for griffon vultures (*Gyps fulvus*; blue square) against a dark grey background with three white blades (A, pattern 'white'), two white blades and one black blade (B, pattern 'black'), three striped blades (C, pattern 'striped'), or three checkered blades (D, pattern 'checkered'). The dotted red line represents the detection threshold (binomial test, $p < 0.05$): all points below this line indicate a combination of pattern $\times$ speed where the vulture failed to discriminate between the stationary and rotating turbines.

Table SM.B1. Models performed for likelihood ratio tests comparisons. Columns show the model structure (interactions between pattern (P), speed (S) and background (B) are indicated by $\times$), model degrees of freedom (Model df), Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), log-likelihood and deviance. All models included session date and individual identity as random effects.

Table SM.B2. Results of the likelihood ratio tests performed to compare the full model to reduced models from which specific interaction terms were removed. Columns show the model's name (see Table S1), the likelihood ratio chi-square statistic (Chi-square), the degrees of freedom for the test (Test df) and the associated *p* value.

Table SM.B3. Results of the retained binomial generalized linear mixed model. Effects are reported relative to white (reference pattern) and light grey (reference background). The table reports, for each model term, the estimated coefficient, its standard error, *z* value and *p* value.

Table SM.B4. Results of the pairwise comparison performed between patterns at each speed level, applying a Bonferroni correction for multiple testing. Columns show the odds ratio for each pattern comparison, its standard error, the *z*-ratio and the Bonferroni-adjusted *p* value.

Table SM.C1. Models performed for likelihood ratio tests comparisons. Columns show the model structure (interactions between pattern (P), speed (S) and background (B) are indicated by x), model degrees of freedom (Model df), Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), log-likelihood and deviance. All models included session date and individual identity as random effects.

Table SM.C2. Results of the likelihood ratio tests performed to compare the full model to reduced models from which specific interaction terms were removed. Columns show the model's name (see Table S5), the likelihood ratio chi-square statistic (Chi-square), the degrees of freedom for the test (Test df) and the associated *p* value.

Table SM.C3. Results of the retained binomial generalized linear mixed model. Effects are reported relative to white (reference pattern) and light grey (reference background). The table reports, for each model term, the estimated coefficient, its standard error, *z* value and *p* value.

Table SM.C4. Results of the pairwise comparisons performed on the retained model between pattern. Odds ratios are reported with standard errors (SE), degrees of freedom (df), *t* ratios and Bonferroni-adjusted *p* values.

Figure S1. Visual of the pattern design of the three turbine blades. In the striped pattern, the 6.5-cm stripes were separated by 13 cm. In the checkered pattern, the 2-cm² squares were separated by 1 cm in the inner third of the blades, by 2 cm in the second third and by 3 cm in the outer third of the blades. For both 'stripes' and 'checkered', the positions of the stripes or squares were shifted from one blade to another so that no pattern elements overlapped between blades.

Figure S2. Percentage of bird success in discriminating the stationary from the rotating turbine as a function of rotation speed for domestic pigeons (*Columba livia domestica*; light green circle) and black kites (*Milvus migrans*; light brown diamond) against a light grey background with three white blades (A), two white blades and one black blade (B), three striped blades (C), or three checked blades (D). Mean values ($\pm$ SE) are shown for pigeons (dark green circle) and kites (dark brown diamond). The dotted red line represents the detection threshold (binomial test, $p < 0.05$): all points below this line indicate a pattern $\times$ speed combination where the birds failed to discriminate between the stationary and rotating turbines.

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