Herpetological Conservation and Biology 19(2):289–302.
Submitted: 15 April 2024; Accepted: 10 July 2024; Published: 31 August 2024.

Reflectance Changes in a Tiny Threatened Gecko do not Impede Computer-Assisted Individual Recognition

Cindy Monnet[1], *Théo Dokhelar*[2], *and Julien Renet*[3,4]

[1]*Conservatoire d'espaces naturels de Provence-Alpes-Côte d'Azur, Pôle Biodiversité régionale, 18 Avenue du Gand, 04200 Sisteron, France*
[2] *Centre d'Ecologie Fonctionnelle et Evolutive, Université de Montpellier, Centre National de la Recherche Scientifique, Ecole Pratique des Hautes Etudes, Institut de Recherche pour le Développement, 34000 Montpellier, France*
[3] *Fauna Studium, Scientific Consulting, 25 Avenue du Jabron, 04200 Sisteron, France*
[4]*Corresponding author, email: julien.renet13@hotmail.fr*

***Abstract*.—Photo-identification is widely used for individual recognition in capture-recapture wildlife monitoring; however, the rapid coloration changes exhibited by some species may mask their distinct body patterns and lead to misidentifications. This is especially true for many reptiles that may show significant skin darkening or lightening in response to environmental variations. In this study, we assessed the effect of total dorsal reflectance changes of threatened European Leaf-toed Geckos (*Euleptes europaea*) on the performance of Wild-ID and Hotspotter, two of the most commonly used individual recognition software for wildlife monitoring. We exposed 30 European Leaf-toed Geckos to two substrate types, natural temperature, and light variations to induce coloration changes and obtain a wide range of reflectance, using standardized measurements. For each gecko, we tested Wild-ID and Hotspotter on two photographic databases (n = 2 × 280) including minimum and maximum reflectance differences. In both conditions, Wild-ID and Hotspotter proved to be extremely reliable with a 100% recognition rate. The analysis of similarity scores further suggested that Hotspotter is less sensitive to reflectance changes than Wild-ID. Our results provide the first evidence that significant darkening does not impede computer-assisted individual recognition. We advocate the use of Hotspotter for monitoring populations of European Leaf-toed Geckos. This study should motivate biologists to evaluate the effectiveness of this individual recognition software on other saurian species whose body patterns may be concealed by pronounced changes in reflectance.**

Key Words.—*Euleptes europaea*; European Leaf-toed Gecko; Hotspotter; photographic identification; physiological color change; similarity score; total reflectance; Wild-ID

Introduction

Photo-identification is a non-invasive and low-cost method widely used in capture-recapture wildlife monitoring (Bengsen et al. 2011; Başkale and Kaya 2012; Pace et al. 2017; Schofield et al. 2020). It limits the pain and discomfort caused by more invasive individual marking techniques (e.g. toe clipping) to only the stress induced by the capture and photography of the individual. This method, however, requires distinctive body patterns (e.g. spots, stripes, notches) from the studied species that remain stable over time (Bolger et al. 2012). Although visual matching of photos is considered a valid methodology to monitor small populations during limited time periods, it can become tedious, time consuming, and prone to misidentifications when used to monitor large populations over several years (Morrison et al. 2011; Cruickshank and Schmidt 2017). To increase efficiency and reliability of individual recognition, several pattern recognition algorithms have been developed and integrated into photo-identification software. Such software allows users to automate the matching between two images of the same individual based on characteristic body patterns or easily identifiable morphological features (e.g., scale morphology; Sacchi et al. 2016). Based on the Scale-Invariant Feature Transform (SIFT) algorithm, Wild-ID (Bolger et al. 2012) and Hotspotter (Crall et al. 2013) are two of the most used open-source individual recognition software for the study of animal population dynamics.

Body patterns are not always visible in species showing physiological color changes. This phenomenon is induced by the movement (dispersion or aggregation) of pigment granules in the chromatophores in a fast process that can take only a few seconds (Bagnara and Hadley 1973). A common example in reptiles is the movement of melanosomes (organelles containing melanin pigment) within melanophores,

Figure 1. An adult male European Leaf-toed Geckos (*Euleptes europaea*) moving on a Eucalyptus (*Eucalyptus* sp.) tree on the Ile du Levant (Var, France). (Photographed by Julien Renet).

which enables them to darken their skin by dispersing melanosomes to increase heat absorption or lighten their skin by contracting melanosomes to avoid overheating (Langkilde and Boronow 2012; Smith et al. 2016). Such reflectance changes can also occur in response to stress (Boyer and Swierk 2017; Lewis et al. 2017) or social interactions (Stuart-Fox and Moussalli 2008; Ligon and McGraw 2013; Ligon 2014). Significant skin darkening may, however, obscure body patterns, increasing the risk of misidentification and bias in demographic estimates. No quantitative studies have been conducted to assess the impact of color changes on individual algorithmic recognition.

European Leaf-toed Geckos (*Euleptes europaea*) are the smallest European geckos (snout-vent length < 5 cm) and are endemic to the western Mediterranean area (Delaugerre 1997). Melanophores are mainly responsible for the pigmentation of the species (Delaugerre 1981). The dorsum, with cream to black pigmentation, has a constellation of lighter scales (Fig. 1). A pale dorsal line with light transverse bands is usually found on the back of individuals. This species has the particularity of reflectance changes, from a light to a darker coloration, revealing or attenuating the dorsal patterns. Despite being classified as Near Threatened on a global scale (Corti et al. 2009) and Endangered in the French region Provence-Alpes-Côte d'Azur (Marchand et al. 2017), no individual-level population monitoring has been conducted due to the lack of acceptable permanent marking techniques. The small size of the species precludes the use of transponders, while color markings, which are generally used for short-term recognition (Salvidio and Delaugerre 2003; Salvidio and Oneto 2008; Costa et al. 2019; Radi and Zuffi 2022), are not persistent due to the molting phenomenon and rubbing in crevices.

We evaluated the reliability of Wild-ID and Hotspotter on European Leaf-toed Geckos. For this purpose, we kept 30 captive geckos in the field, exposing them to two substrate types, natural temperature, and light conditions, to collect dorsal photographs at different reflectance levels. We then estimated error rates of Wild-ID and Hotspotter under minimum and maximum reflectance differences. We compared the results for each software between both conditions and provided recommendations for the individual monitoring of European Leaf-toed Geckos.

Materials and Methods

Experimental design.—To collect dorsal photographs of the European Leaf-toed Geckos at different reflectance levels, we captured 30 adults (13 males and 17 females) in May 2021 on the islet of La Tradelière in the French Lérins archipelago (43°30'58.686"N, 7°4'21.226"E). We kept the individuals in captivity for four consecutive nights and days in six 35 × 27 × 30 cm terraria installed outdoors at the capture site, away from direct sunlight. Each terrarium contained a group of five individuals (males and females combined). We kept these groups together for the duration of the experiment. During captivity, we fed the individuals with invertebrates collected on the islet of La Tradelière. We released all individuals in the area of their capture on the fourth day.

We coated the four walls of the three terraria with light-colored cement and lined the bottom with mineral material from the islet La Tradelière. Using glue, we covered the four walls of the other three terraria with topsoil and placed plant material, collected on La Tradelière, in the bottom of the boxes. We also equipped all terraria with two transparent Plexiglas walls perforated for aeration. This experimental design allowed us to mimic two micro-habitats used by European Leaf-toed Geckos: a light-colored rocky micro-habitat and a dark-colored vegetated micro-habitat. Throughout the experiment, we exposed each group of individuals equally to both substrate types (for more details, see Appendix Text). Because we placed the terraria outdoors, the groups of individuals were exposed to the natural day/night cycle (i.e. under natural light) as well as local temperature variations. While reflectance change in reptiles is typically associated with thermoregulation, studies in controlled conditions suggest that background matching and light effects are predominant in two

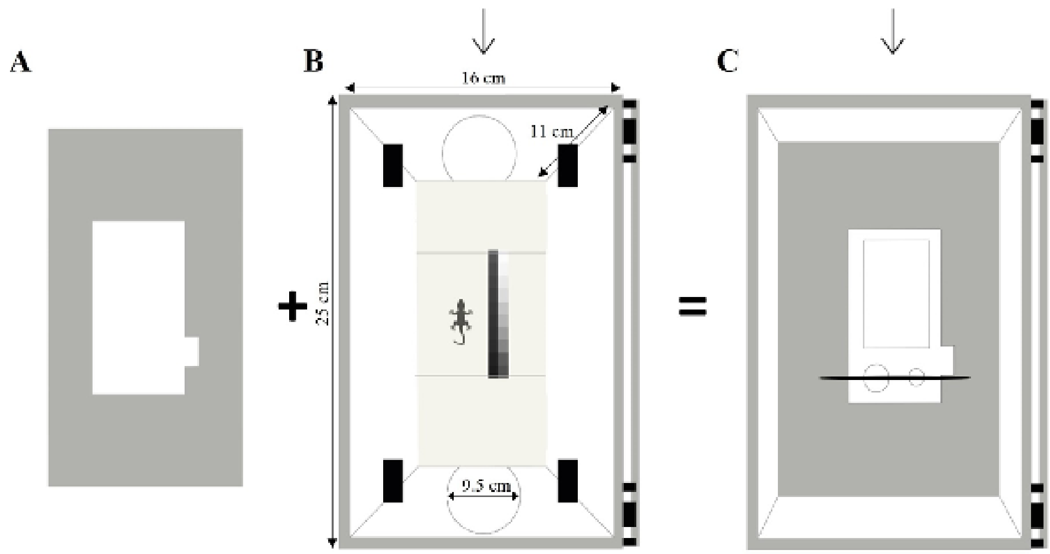


Figure 2. Characteristics of the portable photographic studio (25 ×16 × 11 cm) allowing the standardization of shots. (A) Base for the digital camera. (B) Background of the photographic studio where the individual is held next to the greyscale. The arrows indicate the holes (9.5 cm diameter) for passing the hands and holding the animal. (C) Digital camera base added for shooting.

gecko species: the Mediterranean House Gecko (*Hemidactylus turcicus*; Zaidan and Wiebusch 2007) and the Moorish Gecko (*Tarentola mauritanica;* Vroonen et al. 2012). Exposing European Leaf-Toed Geckos to variations in temperature, background, and light maximized the chances of obtaining a wide range of reflectance in a species for which the factors influencing coloration changes are poorly understood.

We inscribed a number on the side of the individuals using a non-toxic edding® brand paint pen (edding International GmbH, Ahrensburg, Germany) for individual recognition. We assessed reflectance changes from photographs of the dorsal surface of individuals. We took dorsal photographs from the first night (capture of the individuals) to the fourth and last day (release of the individuals), excluding the first day to allow the geckos to acclimate in the terraria. We always photographed lizards during the same time slot (at 1230 and at 2330). To capture images of their dorsum, we gently removed geckos from their terraria and positioned them in a photographic studio offering standardized conditions (position of the animal, distance between the digital camera and the animal, angle of view, luminosity; Fig. 2, Appendix Table 1). A first handler held the gecko while a second one took the photograph of the dorsum. The handling of the individuals did not exceed 3 min to minimize stress. We took the photographs in RAW format (dimensions 4,000 × 3,000 pixels) in macro mode using an Olympus® TG-6 camera equipped with an LG-1 LED ring (OM Digital Solutions Corporation, Tokyo, Japan).

Reflectance analysis.—The dorsal coloration of *E. europaea* is mainly determined by melanophores resulting in achromatic and neutral colors (black, white, gray). Hence, this study is based on total reflectance, which refers to the ability of individuals to lighten (higher reflectance) and darken (lower reflectance) their coloration, without reference to chroma. We measured total reflectance from digital photographs, using the method developed by Hamilton et al. (2008). The darkness of a body area is determined by measuring the percentage of reflected white light, through a comparison of the coloration pattern with a standard gray scale. Using a photograph, the reflectance of each pixel is measured, ranging from 0 (black) to 1 (white) and corresponding to a reflectance of 0 to 100%. The average reflectance is then defined as the sum of the reflectance values of all pixels included in the selection divided by the number of pixels. Each day and night, excluding the first day, we determined the average total dorsal reflectance of each of the 30 tagged geckos. In this way, we identified the pairs of images exhibiting the maximum and minimum reflectance differences for each individual (Appendix Table 2).

We converted all photographs to TIFF format using XnConvert 1.90.0 (XnSoft Corp., Reims, France). We measured total reflectance of the dorsum of geckos in ImageJ 1.53a (Schneider et al. 2012). We first standardized images to 8-bit greyscale and then calibrated them using the standard Tiffen Q-13 greyscale positioned next to each individual, with 20 shades representing grey reflectance values equal to 0.891 (89.1%) down to 0.011 (1.1%) (Fig. 2). We extracted the average total reflectance of the dorsum of the lizard by delineating the contours of the back, from the humerus to the iliosacral joint area. The reflectance of the terrarium walls, measured from one rocky micro-habitat and one vegetated micro-habitat terrarium, corresponded to 0.386 and 0.071, respectively.

Software for individual recognition.—*Wild-ID*: Wild-ID (Bolger et al. 2012) uses the SIFT algorithm (Lowe 2004) to identify distinctive features in each greyscale transformed image. It then evaluates pattern similarities for each pair of images by comparing the arrangement of SIFT features. A similarity score is then computed based on how well the features of the two images fit. Wild-ID provides the observer with 20 candidates, the best being the one with the highest score (a score of 1 indicating a perfect match). It is recommended to crop the images on the body area of interest with another software to eliminate spurious features in the background. Thus, for the use of Wild-ID, we cropped dorsal photographs of geckos using XnView 2.49.3 software (XnSoft Corp., Reims, France).

Hotspotter: Hotspotter (Crall et al. 2013) uses two algorithms. First, a one-versus-one algorithm, comparable to SIFT, extracts SIFT features based on RootSIFT (Arandjelović and Zisserman 2012) and the Hessian-Hessian operator (Perd'och et al. 2009). Second, a one-versus-many algorithm employs LNBNN methods to identify images with similar groupings of features. While the one-versus-one matching algorithm compares the query image against each database image sequentially, the one-versus-many matching algorithm compares each descriptor from the query image against all descriptors from the image database. Based on the results of both algorithms, Hotspotter assigns a similarity score to each match. By default, it proposes five candidates (which can be adjusted by the user), the best candidate having the highest score. Unlike Wild-ID, Hotspotter includes a tool for cropping the images to the region of interest, called chips. For both Wild-ID and Hospotter, the user is presented with suggested candidates and must visually compare them to the subject individual, deciding whether or not there is a match.

Wild-ID and Hotspotter evaluation procedure.— To assess the effect of reflectance changes on the performance of Wild-ID and Hotspotter, we conducted the analyses using dorsum photographs with maximum and minimum individual reflectance differences. Thus, we created two photographic databases for each of the 30 individuals identified by photograph number and paired for both reflectance levels (i.e., minimum and maximum; Appendix Figure). We standardized all the photographs collected for this study under the same conditions (Fig. 2, Appendix Table 1), despite the diversity of localities. Because Wild-ID and Hotspotter do not support RAW and TIFF image formats, we converted all images selected for photo-identification analyses to JPEG using XnConvert 1.90.0 (XnSoft Corp., Reims, France).

The first database aimed to assess the ability of the software to recognize the individual when the reflectance difference was at a minimum. This database consisted of 249 photographs of individual *E. europaea* collected by our team prior to this study in various localities (Riou, Frioul, and Lerins archipelagos) and therefore distinct from the 30 geckos studied. First, we included a photograph of each of the 30 individuals studied showing minimum reflectance differences representing a photographic base of 279 different individuals. We then added one by one the second photograph corresponding to the image pair of the individuals studied and launched a recognition analysis for each new inclusion. After obtaining the result (i.e., ranks and similarity scores) the photograph of the individual studied was replaced by the photograph of a new individual so as to maintain a numerically stable database for each individual (i.e., one image vs. 279) for both software packages (Appendix Figure).

We created the second database to assess the ability of the software to recognize each of the 30 individuals studied when the reflectance difference was at a maximum. This compilation also incorporates the same 249 photographs collected from various locations before this study. The process followed an identical protocol, although under conditions of maximum reflectance difference (Appendix Figure). The comparison analysis was carried out 120 times (i.e., 60 times for each software tested).

We quantified the error rates by calculating the False Rejection Rate (FRR) for the top-ranking candidate. The FRR corresponds to the probability that a recapture event is falsely identified as a new capture (i.e., the software fails to match two

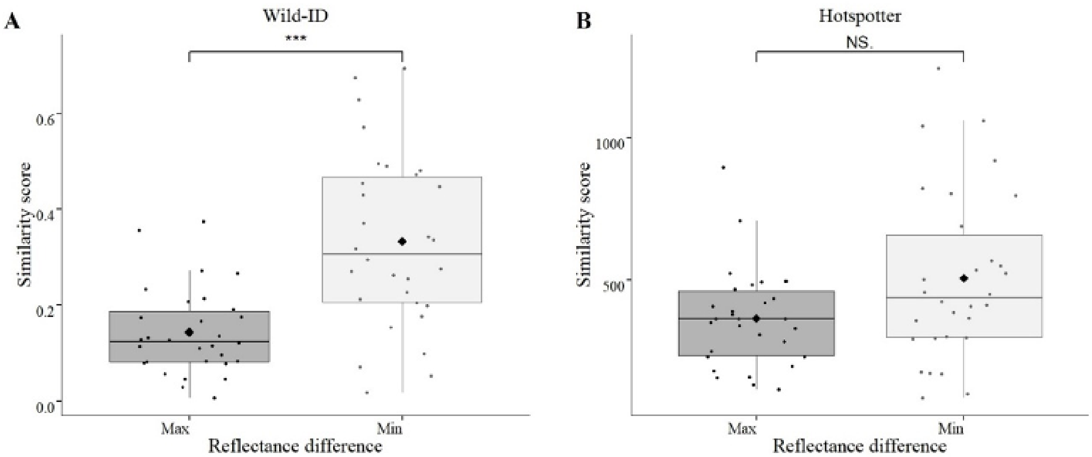


Figure 3. Similarity scores of European Leaf-toed Geckos (*Euleptes europaea*) obtained for (A) Wild-ID and (B) Hotspotter in maximum (Max) and minimum (Min) reflectance difference conditions. The abbreviation NS = not significant and three asterisks (***) = significant difference ($P < 0.001$). Black diamonds represent the means of the similarity scores. The higher the score, the greater the similarity between the two potential matches.

photographs of the same individual; Jain 2007; Morrison et al. 2011; Bolger et al. 2012; Bendik et al. 2013; Dunbar et al. 2014). FRR is calculated as the ratio between the number of false rejections and the total number of identification attempts, and thus ranges from 0 (100% success in matching two different images) to 1 (0% success).

Because data failed to approximate normal distribution, we used a non-parametric Wilcoxon-Mann-Whitney test to evaluate the differences between the similarity scores obtained by the same software in conditions of maximum and minimum reflectance differences. The comparison of the similarity scores between Wild-ID and Hotspotter could not be performed because each software has a specific method of calculating the scores (Appendix Figure). We performed analyses using R software, v.4.1.0 (R Development Core Team 2021) and we generated plots with the ggplot2 package (Wickham 2016).

Results

The total dorsal reflectance of the 30 European Leaf-toed Geckos varied from a minimum of 0.088 and maximum of 0.310 (median = 0.190). The mean reflectance was 0.189 ± 0.047 (standard deviation). For Wild-ID and Hotspotter, the top ranked candidate was always the true matching image for both minimum and maximum reflectance differences (FRR = 0). Thus, both software packages correctly recognized the image pairs for each individual. For Wild-ID, the scores obtained for maximum reflectance differences (mean = 0.143 ± 0.090) were significantly lower than minimum reflectance differences (mean = 0.333 ± 0.182; $W = 165$, $P < 0.001$; Fig. 3). Conversely, for Hotspotter, the similarity scores obtained for maximum reflectance differences (mean = 364.9 ± 170.1) were not significantly different from the scores obtained for minimum reflectance differences (mean = 506.9 ± 297.6; $W = 321.5$, $P = 0.057$; Fig. 3).

Discussion

Consequences of reflectance changes on algorithmic performance.—Our study is the first to investigate the use of photographic identification for individuals subject to physiological color change, specifically focusing on the ability of the European Leaf-toed Gecko to darken and lighten their skin. With a 100% success rate (FRR = 0) in the top-ranking candidate match for both minimum and maximum reflectance differences, Wild-ID and Hotspotter proved to be extremely reliable in recognizing individual European Leaf-toed Geckos. Despite the large reflectance differences, both software programs were highly successful in identifying SIFT features and matching them (Fig. 4). By performing a series of image transformations including greyscale conversion, contrast, and brightness adjustment (Lowe 2004), SIFT algorithm allows the dorsal patterns (i.e. pale dorsal line and transverse bands) to reappear. Thus, the SIFT algorithm seems to identify the contours of the patterns by selecting the darkest scales, contrasting with the light dorsal patterns. Other studies have shown that SIFT algorithm relies

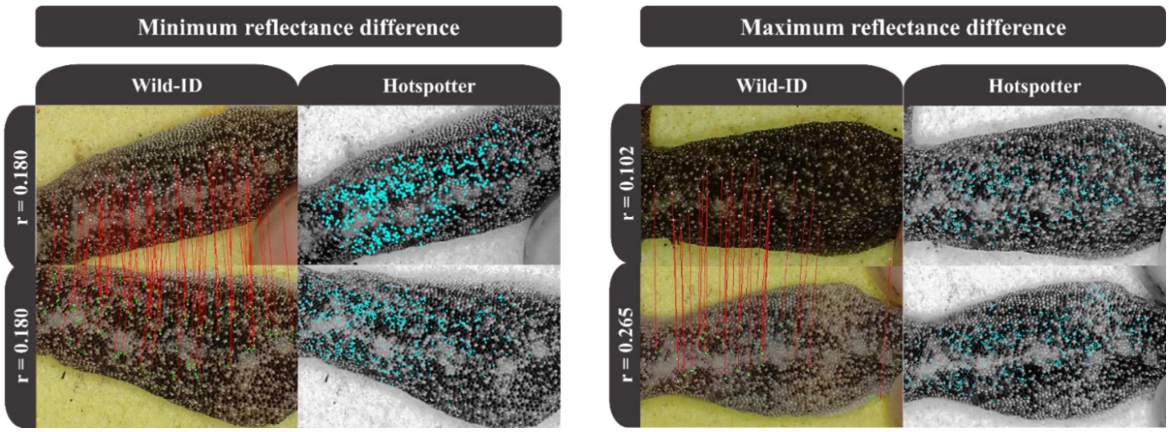


Figure 4. The SIFT features extracted by Wild-ID (white points) and Hotspotter (blue points) for European Leaf-toed Geckos (*Euleptes europaea*) that are similar for the image pair of individual 13 in minimum and maximum reflectance difference condition. The reflectance (*r*) is specified for the investigated individual (top) and the suggested candidate by the software (bottom). The red lines connect the SIFT features identified by Wild-ID and the green points correspond to the location where the SIFT features of the suggested candidate should be after affine transformation of the investigated individual. Note that Wild-ID does not provide a visual of the greyscale images.

on the most contrasting patterns of the photograph (i.e., with large reflectance differences) that can be easily localized (e.g., giraffe spot contours, zebra stripe contours; Bolger et al. 2012; Crall et al. 2013). The contrasting patterns between dark (lighter insertions) and light (darker insertions) scales may facilitate recognition of individuals by the algorithm, potentially explaining this very high recognition rate of both software types on the species.

Because scale shapes and combinations are individual-specific and generally stable over time for adults, many researchers have already relied on these features for individual identification in reptiles (Steinicke et al. 2000; Perera and Pérez-Mellado 2004; Sacchi et al. 2010; Rotger et al. 2019; Hoefer et al. 2021). When photo-identification software is used, however, it often requires a pre-processing step by manually defining scale edges and vertexes (Sacchi et al. 2016). The application of automated photo-identification software incorporating the SIFT algorithm in reptiles has received limited exploration, with most studies focusing on turtle species (Cross et al. 2014; Long and Azmi 2017; Suriyamongkol and Mali 2018; Dunbar et al. 2021; Tabuki et al. 2021). Interestingly, for studies based on turtle face identification, SIFT appears to rely on the scale contours (Dunbar et al. 2021). Sacchi et al. (2016) warned that the application of individual photo-identification could be difficult in some taxa, particularly in geckos because they exhibit similar morphologies in scale structuring. Therefore, gecko photo-identification is usually based on visual comparisons of color patterns (Wanger et al. 2008; Knox et al. 2013; Hoare et al. 2013; Lettink and Monks 2016; Chœur et al. 2023). Recently, Gewiss et al. (2021) demonstrated the success of Wild-ID for individual recognition of yellow reticulations in the Psychedelic Rock Gecko (*Cnemaspis psychedelica*). Our study highly suggests that scale structure may play an important role in individual recognition in *E. europaea*, and coupled with contrasting pigmentary patterns, provides reliable algorithmic individual recognition. Further studies on reptiles showing pronounced reflectance changes would allow a better assessment of the role of skin structure in computer-assisted individual recognition.

Similarity score analyses revealed small variations in the performance of the two software packages in recognizing individuals of European Leaf-toed Geckos. Wild-ID displayed significantly lower similarity scores for maximum reflectance differences compared to minimum reflectance differences. In contrast, Hotspotter's similarity scores did not differ significantly between the two reflectance conditions. This finding indicates that Hotspotter is less sensitive to reflectance changes than Wild-ID, and therefore may be less likely to generate false rejection errors as sample sizes of unknown individuals increase. The combination of the two algorithms, one-versus-one and one-versus-many, probably provides Hotspotter with a highly reliable identification procedure. Such performance differences between the two software (Wild-ID vs Hotspotter) were also attested by several authors in mammalian species (Crall et al. 2013; Chehrsimin et al. 2018; Nipko et al. 2020).

A major limitation of our study is the very short time interval between each photograph (maximum 4 d), which does not allow for the evaluation of the timescale of photo-identification reliability. Additionally, we only focused on adult specimens. If scale pigmentation appears to be a criterion used by the SIFT algorithm, this trait may change over time, particularly during ontogenetic development. Some authors have noted a negative relationship between similarity scores and the increasing time intervals marked by the evolution of natural color marks in amphibians (Bendik et al. 2013; Bardier et al. 2020). Morphological color changes, however, occurring on facial scutes do not prevent the individual recognition of juvenile sea turtles (Chew et al. 2015; Carpentier et al. 2016; Dunbar et al. 2021), suggesting that stable arrangement of large scales allow for reliable identification. Current documentation on the evolution of scales, both morphologically and pigmentally, throughout the life cycle of the European Leaf-toed Gecko is very poor. Assessing the reliability of computer-assisted photo-identification over a longer time scale would allow evaluation of features stability in adults and determination of the minimum age or body size for a successful use.

Conclusion.—When monitoring species with computer-assisted photo-identification, the standardization of photographs is imperative to obtain sharp and high-quality images (Kelly 2001; Bendik et al. 2013; Morrison et al. 2016; Sacchi et al. 2016), which will be more likely to match (Nipko et al. 2020). For this purpose, the use of a portable photographic studio comparable to the one suggested here for monitoring a small gecko is essential to ensure safe handling and stability of photographic parameters (i.e., consistent angle of view, distance between the animal and the camera, non-reflected light). With such a device, two people are enough to hold and photograph the individuals in the field. Within the framework of a capture-recapture study of European Leaf-toed Geckos, we advise to carry out the photographs at night to conform with the activity time of this species.

Hotspotter offers more options and tools to ease the pre-processing of images and their analysis (Nipko et al. 2020; Dunbar et al. 2021). The creation of chips allows for quick extraction of the region of interest from the photographs being compared without relying on any external software. The orientation of the animal can also be defined, allowing oblique postures. Users can visualize the SIFT features on which Hotspotter relies to compare images. Such software can integrate individuals over the course of capture-recapture sessions without the need to reprocess old photographs, unlike Wild-ID. The user can label identified individuals for referencing. The automated greyscale conversion of the chips makes the visual recognition of European Leaf-toed Geckos possible and allows the user to make the final decision (i.e., if the candidate suggested by the software corresponds or not to the investigated individual). In light of all these advantages, Hotspotter appears to be the ideal software for the demographic monitoring of the European Leaf-toed Geckos. As a first step, conducting field studies with increasing time intervals (e.g., several months, then several years) would allow verifying the reliability of Hotspotter in real conditions. A next step may be to assess its effectiveness on younger age classes. A better understanding of the population dynamics will allow the implementation of relevant conservation actions for this threatened species.

Acknowledgments.—We warmly thank Amanda Xérès (Conservatoire d'espaces naturels de Provence-Alpes-Côte d'Azur), Félix Thirion (Conservatoire d'espaces naturels de Provence-Alpes-Côte d'Azur), Nathan Huvier, Corentin Lambert-Grimpard (Muséum d'Histoire Naturelle de Nice), Alexandre Viguier (Office Français de la Biodiversité) for their assistance in the field and Olivier Gerriet (Muséum d'Histoire Naturelle de Nice) who designed the terraria and helped us on the field. Our study was made possible thanks to the logistical support of the Office National des Forêts (Eric Tassone) and the Parc National des Calanques (Lidwine Le Mire Pecheux, Lorraine Anselme, Alain Mante and Timothée Cuchet). We also thank Thomas Morrison (University of Glasgow), Jonathan Crall (Kitware Inc.), Agata Staniewicz (University of Bristol), Maximilian Matthé (University of Dresden), Aurélien Besnard (CNRS Montpellier), Hugo Cayuela (Université de Lyon) and Giacomo Rosa (University of Genoa) for providing useful comments which helped to significantly improve the quality of the manuscript. The English translation was assisted by Félix Thirion, whom we sincerely thank. Figure 2 was illustrated by Théo Xérès. This work was funded by the Provence-Alpes-Côte d'Azur region, the Bouches-du-Rhône departmental council and supported by the Conservatoire d'espaces naturels de Provence-Alpes-Côte d'Azur and the Parc National des Calanques. Our study was authorized by the French government by prefectural decree for the departments of Alpes-Maritimes (permit number: 2020_341) and Bouches-du-Rhône (permit number: 2020_250 and 2021_113).

Literature Cited

Arandjelović, R., and A. Zisserman. 2012. Three things everyone should know to improve object retrieval. Pp. 2911–2918 *In* 2012 IEEE Conference on Computer Vision and Pattern Recognition. Institute of Electrical and Electronics Engineers, Providence, Rhode Island, USA.

Bagnara, J.T., and M.E. Hadley. 1973. Chromatophores and Color Changes: The Comparative Physiology of Animal Pigmentation. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Bardier, C., D. Székely, G. Augusto-Alves, N. Matínez-Latorraca, B.R. Schmidt, and S.S. Cruickshank. 2020. Performance of visual vs. software-assisted photo-identification in mark-recapture studies: a case study examining different life stages of the Pacific Horned Frog (*Ceratophrys stolzmanni*). Amphibia-Reptilia 42:17–28.

Başkale, E., and U. Kaya. 2012. Decline of the Levantine Frog, *Pelophylax bedriagae* Camerano, 1882, in the western Aegean Region of Turkey changes in population size and implications for conservation. Zoology in the Middle East 57:69–76.

Bendik, N.F., T.A. Morrison, A.G. Gluesenkamp, M.S. Sanders, and L.J. O'Donnell. 2013. Computer-assisted photo identification outperforms visible implant elastomers in an endangered salamander, *Eurycea tonkawae*. PLoS ONE 8:1–8. https://doi.org/10.1371/journal.pone.0083953.

Bengsen, A., J. Butler, and P. Masters. 2011. Estimating and indexing feral cat population abundances using camera traps. Wildlife Research 38:732–739.

Bolger, D.T., T.A. Morrison, B. Vance, D. Lee, and H. Farid. 2012. A computer-assisted system for photographic mark-recapture analysis. Methods in Ecology and Evolution 3:813–822.

Boyer, J.F., and L. Swierk. 2017. Rapid body color brightening is associated with exposure to a stressor in an *Anolis* lizard. Canadian Journal of Zoology 95:213–219.

Carpentier, A.S., C. Jean, M. Barret, A. Chassagneux, and S. Ciccione. 2016. Stability of facial scale patterns on Green Sea Turtles *Chelonia mydas* over time: a validation for the use of a photo-identification method. Journal of Experimental Marine Biology and Ecology 476:15–21.

Chehrsimin, T., T. Eerola, M. Koivuniemi, M. Auttila, R. Levänen, M. Niemi, M. Kunnasranta, and H. Kälviäinen. 2018. Automatic individual identification of Saimaa ringed seals. IET Computer Vision 12:146–152.

Chew, V.Y.C., H.C. Liew, and J. Joseph. 2015. Photographic identification of green turtles (*Chelonia mydas*) at Redang Island, Malaysia. Marine Turtle Newsletter 146:1–6.

Chœur, A., J. Clémencet, M. Le Corre, M.A. Roesch, and M. Sanchez. 2023. Intra-annual variations of microhabitat use and movements of a critically endangered arboreal day gecko endemic to Reunion Island: implications for conservation. Amphibia-Reptilia 44:139–152.

Corti, C., M. Cheylan, P. Geniez, R. Sindaco, and A. Romano. 2009. *Euleptes europaea* (Gené, 1839*)*. The IUCN Red List of Threatened Species 2009. International Union for Conservation of Nature. http://www.iucnredlist.org.

Costa, A., F. Oneto, and S. Salvidio. 2019. Time-for-space substitution in N-mixture modeling and population monitoring. Journal of Wildlife Management 83:737–741.

Crall, J.P., C.V. Stewart, T.Y. Berger-Wolf, D.I. Rubenstein, and S.R. Sundaresan. 2013. Hotspotter - Patterned species instance recognition. Pp. 230–237 *In* 2013 IEEE Workshop on Applications of Computer Vision. Institute of Electrical and Electronics Engineers, Clearwater Beach, Florida, USA.

Cross, M.D., Jr., G.J. Lipps, J.M. Sapak, E.J. Tobin, and K.V. Root. 2014. Pattern-recognition software as a supplemental method of identifying individual Eastern Box Turtles (*Terrapene c. carolina*). Herpetological Review 45:584–586.

Cruickshank, S.S., and B.R. Schmidt. 2017. Error rates and variation between observers are reduced with the use of photographic matching software for capture-recapture studies. Amphibia-Reptilia 38:315–325.

Delaugerre, M. 1997. *Phyllodactylus europaeus*. Pp. 212–213 *In* Atlas of Amphibians and Reptiles in Europe. Gasc, J.-P., A. Cabela, J. Crnobrnja-isailovic, D. Dolmen, K. Grossenbacher, P. Haffner, J. Lescure, H. Martens, J.-P. Martìnez Rica, H. Maurin, M.-E. Oliveira, T. Sofianidou, M. Veith, and A. Zuiderwijk (Eds.). Societas Europea Herpetologica and Muséum national d'Histoire naturelle, Paris, France.

Delaugerre, M. 1981. Un cas d'albinisme chez *Phyllodactylus europaeus* Gene, 1838. Premier cas signalé dans la famille des *Gekkonidae* (*Sauria*-Reptiles). Bulletin Mensuel de la Société Linnéenne de Lyon 50:213–216.

Dunbar, S.G., E.C. Anger, J.R. Parham, C. Kingen, M.K. Wright, C.T. Hayes, S. Safi, J. Holmberg, L. Salinas, and D.S Baumbach. 2021. HotSpotter: using a computer-driven photo-id application to identify sea turtles. Journal of Experimental Marine Biology and Ecology 535:1–11. https://doi.org/10.1016/j.jembe.2020.151490.

Dunbar, S.G., H.E. Ito, K. Bahjri, S. Dehom, and L. Salinas. 2014. Recognition of juvenile Hawksbills *Eretmochelys imbricata* through face scale digitization and automated searching. Endangered Species Research 26:137–146.

Gewiss, L.R., H.N Ngo, M. van Schingen-Khan, K.V. Nguyen, T.Q. Nguyen, A. Rauhaus, and T. Ziegler. 2021. Photographic Identification of *Cnemaspis psychedelica*: a useful tool to improve the regulation of international wildlife trade. Herpetological Conservation and Biology 16:142–149.

Hamilton, P., D.E. Gaalema, and B. Sullivan. 2008. Short-term changes in dorsal reflectance for background matching in Ornate Tree Lizards (*Urosaurus ornatus*). Amphibia-Reptilia 29:473–477.

Hoare, J.M., P. Melgren, and E.E. Chavel. 2012. Habitat use by southern forest geckos (*Mokopirirakau* ‘Southern Forest’) in the Catlins, Southland. New Zealand Journal of Zoology 40:129–136.

Hoefer, S., Rotger, A., Mills, S., and N.J. Robinson. 2021. Semi-automated photo-identification of Bahamian Racers (*Cubophis vudii vudii*). Acta Herpetologica 16:133–136.

Jain, A.K. 2007. Biometric recognition. Nature 449:38–40.

Kelly, M.J. 2001. Computer-aided photograph matching in studies using individual identification: an example from Serengeti Cheetahs. Journal of Mammalogy 82:440–449.

Knox, C.D., A. Cree, and P.J. Seddon. 2012. Accurate identification of individual geckos (*Naultinus gemmeus*) through dorsal pattern differentiation. New Zealand Journal of Ecology 37:60–66.

Langkilde, T., and K.E. Boronow. 2012. Hot boys are blue: temperature-dependent color change in male Eastern Fence Lizards. Journal of Herpetology 46:461–465.

Lettink, M., and J.M. Monks. 2016. Survey and monitoring methods for New Zealand lizards. Journal of the Royal Society of New Zealand 46:16–28.

Lewis, A.C., K.J. Rankin, A.J. Pask, and D. Stuart-Fox. 2017. Stress-induced changes in color expression mediated by iridophores in a polymorphic lizard. Ecology and Evolution 7:8262–8272.

Ligon, R.A. 2014. Defeated chameleons darken dynamically during dyadic disputes to decrease danger from dominants. Behavioral Ecology and Sociobiology 68:1007–1017.

Ligon, R.A., and K.J. McGraw. 2013. Chameleons communicate with complex colour changes during contests: different body regions convey different information. Biology Letters 9(6):20130892. https://doi.org./10.1098/rsbl.2013.0892.

Long, S.-L., and N.A. Azmi. 2017. Using Photographic identification to monitor sea turtle populations at Perhentian Islands Marine Park in Malaysia. Herpetological Conservation and Biology 12:350–366.

Lowe, D.G. 2004. Distinctive image features from scale-invariant keypoints. International Journal of Computer Vision 60:91–110.

Marchand, M.A., C. Roy, J. Renet, J. Delauge, D. Meyer, and C. Hayot. 2017. Liste rouge régionale des amphibiens et reptiles de Provence-Alpes-Côte d’Azur. Conservatoire d’espaces naturels Provence-Alpes-Côte d’Azur, Aix-en-Provence, France. 14 p.

Morrison, T.A., D. Keinath, W. Estes-Zumpf, J.P. Crall, and C.V. Stewart. 2016. Individual identification of the endangered Wyoming Toad *Anaxyrus baxteri* and implications for monitoring species recovery. Journal of Herpetology 50:44–49.

Morrison, T.A., J. Yoshizaki, J.D. Nichols, and D.T. Bolger. 2011. Estimating survival in photographic capture-recapture studies: overcoming misidentification error. Methods in Ecology and Evolution 2:454–463.

Nipko, R.B., B.E. Holcombe, and M.J. Kelly. 2020. Identifying individual Jaguars and Ocelots via pattern-recognition software: comparing HotSpotter and Wild-ID. Wildlife Society Bulletin 44:424–433.

Pace, R.M., III, P.J. Corkeron, and S.D. Kraus. 2017. State-space mark-recapture estimates reveal a recent decline in abundance of North Atlantic Right Whales. Ecology and Evolution 7:8730–8741.

Perd’och, M., O. Chum, and J. Matas. 2009. Efficient representation of local geometry for large scale object retrieval. Pp. 9–16 *In* 2009 IEEE Conference on Computer Vision and Pattern Recognition. Institute of Electrical and Electronics Engineers, Miami, Florida, USA.

Perera, A., and V. Perez-Mellado. 2004. Photographic identification as a noninvasive marking technique for Lacertid lizard. Herpetological Review 35:349–350.

R Development Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org.

Radi, G., and M.A.L. Zuffi. 2022. One site, three species, three stories: syntopy of geckoes *Euleptes europaea* (Gené, 1839), *Hemidactylus turcicus* (Linnaeus, 1758), *Tarentola mauritanica* (Linnaeus, 1758) in a coastal area of southern Tuscany (central Italy). Acta Herpetologica 17:187–195.

Rotger, A., V. Colomar, J.E. Moreno, and L. Parpal. 2019. Photo-identification of Horseshoe Whip Snakes (*Hemorrhois hippocrepis*, Linnaeus, 1758) by a semi-automatic procedure applied to wildlife management. Herpetological Journal 29:304–307.

Sacchi, R., S. Scali, M. Mangiacotti, M. Sannolo, and M.A. Zuffi. 2016. Digital identification and analysis. Pp. 59–72 *In* Reptile Ecology and Conservation. A Handbook of Techniques. Dodd, C.K., Jr. (Ed.). Oxford University Press, Oxford, UK.

Sacchi, R., S. Scali, D. Pellitteri-Rosa, F. Pupin, A. Gentilli, S. Tettamanti, L. Cavigioli, L. Racina, V. Maiocchi, P. Galeotti, and M. Fasola. 2010. Photographic identification in reptiles: a matter of scales. Amphibia-Reptilia 31:489–502.

Salvidio, S., and M. Delaugerre. 2003. Population dynamics of the European Leaf-toed Gecko (*Euleptes europaea*) in NW Italy: implications for Conservation. Herpetological Journal 13:81–88.

Salvidio, S., and F. Oneto. 2008. Density regulation in the Mediterranean Leaf-toed Gecko *Euleptes europaea*. Ecological Research 23:1051–1055.

Schneider, C.A., W.S. Rasband, and K.W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9:671–675.

Schofield, G., M. Klaassen, K. Papafitsoros, M.K. Lilley, K.A Katselidis, and G.C. Hays. 2020. Long-term photo-id and satellite tracking reveal sex-biased survival linked to movements in an endangered species. Ecology 101:1–9. https://doi.org/10.1002/ecy.3027.

Smith, K.R., V. Cadena, J.A Endler, W.P Porter, M.R. Kearney, and D. Stuart-Fox. 2016. Colour change on different body regions provides thermal and signalling advantages in Bearded Dragon Lizards. Proceedings of the Royal Society B 283:1–9. https://doi.org/10.1098/rspb.2016.0626.

Steinicke, H., K. Ulbrich, K. Henle, and W.R. Grosse. 2000. Eine neue Methode zur fotografischen Individualidentifikation mittelerupäischer Halsbandeidechsen (Lacertidae). Salamandra 36:81–88.

Stuart-Fox, D., and A. Moussalli. 2008. Selection for social signalling drives the evolution of chameleon colour change. PLoS Biology 6:22–29. https://doi:10.1371/journal.pbio. 0060025.

Suriyamongkol, T., and I. Mali. 2018. Feasibility of using computer-assisted software for recognizing individual Rio Grande Cooter (*Pseudemys gorzugi*). Copeia 106:646–651.

Tabuki, K., H. Nishizawa, O. Abe, J. Okuyama, and S. Tanizaki. 2021. Utility of carapace images for long-term photographic identification of nesting Green Turtles. Journal of Experimental Marine Biology and Ecology 545:1–10. https://doi.org/10.1016/j.jembe.2021.151632.

Vroonen, J., B. Vervust, D. Fulgione, V. Maselli, and R. Van Damme. 2012. Physiological colour change in the Moorish Gecko, *Tarentola mauritanica* (Squamata: Gekkonidae): effects of background, light, and temperature. Biological Journal of the Linnean Society 107:182–191.

Wickham, H. 2016. Ggplot2: Elegant Graphics for Data Analysis. 2nd Edition. Springer, New York, New York, USA.

Wanger, T.C., I. Motzke, S.C. Furrer, B.W. Brook, and B. Gruber. 2008. How to monitor elusive lizards: comparison of capture-recapture methods on Giant Day Geckos (Gekkonidae, *Phelsuma madagascariensis grandis*) in the Masoala rainforest exhibit, Zurich Zoo. Ecological Research 24:345–353.

Zaidan, F., and P.L. Wiebusch. 2007. Effects of temperature and illumination on background matching in Mediterranean Geckos (*Hemidactylus turcicus*). Texas Journal of Science 59:127–136.

Cindy Monnet is a French Herpetologist with a Master's degree in Naturalist Expertise and Biodiversity Management. She has studied and worked on the conservation of several French reptile species within non-governmental organizations such as the Conservatoire d'Espaces Naturels de Provence-Alpes-Côte d'Azur (Sisteron, France) and Nature Environnement 17 (Surgères, France). Currently, Cindy is a Biodiversity Project Manager for the Grand Cognac Agglomeration Community (Cognac, France), where she develops biodiversity preservation programs in collaboration with various local stakeholders. (Photographed by Germain Waroquier).

Theo Dokhelar works as a scientist specializing in herpetology and data analysis. He has extensive experience in conservation biology, particularly in the field of spatial ecology and monitoring protocols. Théo currently works at Centre d'Ecologie Fonctionnelle et Evolutive, Centre National de la Recherche Scientifique, and collaborates with various researchers, associations, and other conservation stakeholders, contributing to the development and evaluation of monitoring protocols and defining conservation management actions. (Photographed by Cindy Monnet).

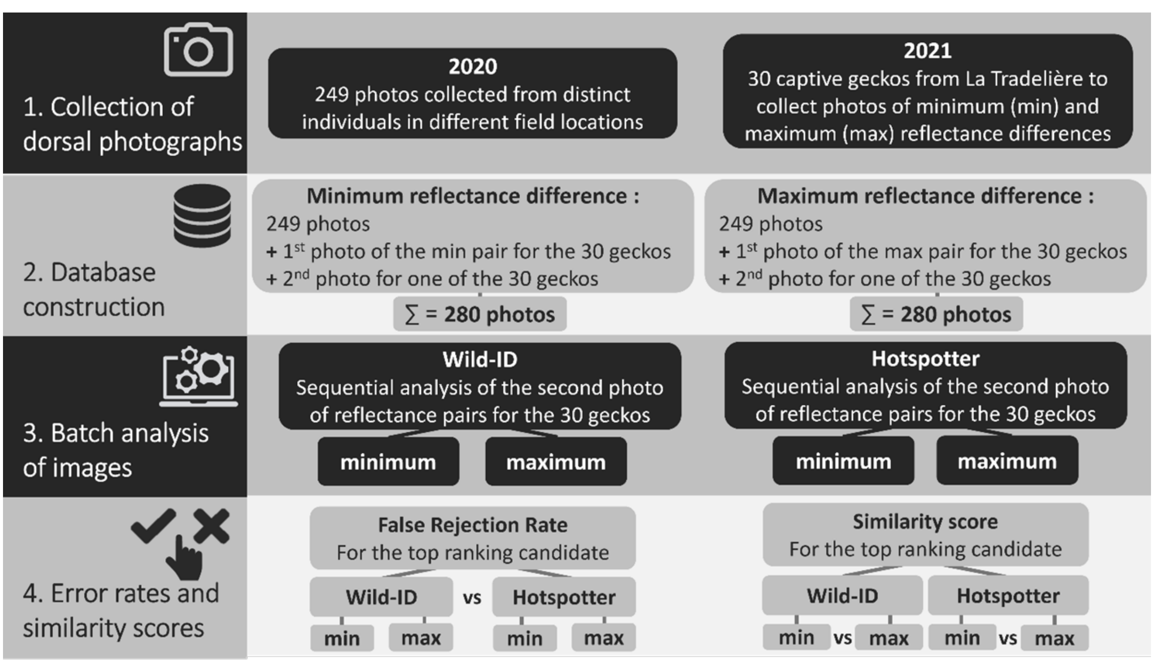
Julien Renet is a French Wildlife Biologist who works as a Scientific Consultant for Fauna studium. For over 10 y, Julien has designed, coordinated, and implemented conservation programs for wildlife. His work concerns the general framework of conservation biology, more specifically spatial ecology, population dynamics, biogeography, and assessments of individual marking methods. (Photographed by Diane Renet).

Appendices

Appendix Text. Experimental design to generate reflectance variations in European Leaf-toed Geckos.

Thirty European Leaf-Toed Geckos (*Euleptes europaea*) were maintained in captivity, distributed equally with five individuals per terrarium. The terraria were organized to mimic two types of micro-habitats: three terraria represented a rocky micro-habitat (RMH) and three represented a vegetated micro-habitat (VMH). The experiment was conducted over four consecutive nights and days, during which groups of individuals were moved between terraria. Specifically, individuals were transferred to the other "type" of micro-habitat on the second day and transferred to another terrarium of the same micro-habitat on the third day.

Dorsal-side photographs (i.e., dorsal-side reflectance) were taken at each session, from night 1 (capture of the individuals) to day 4 (release of the individuals), excluding day 1. On night 1, the geckos were placed in the terraria and not handled on day 1 to allow for acclimatization. Photographs were always taken at thesame times each day (1230 and 2330). After being photographed one last time, the individuals were all released in their original capture area on day 4.



Appendix Figure. Diagram outlining the method used to assess the reliability of Wild-ID and Hotspotter for individual photo-identification of the 30 European Leaf-toed Geckos (*Euleptes europaea)* under minimum (min) and maximum (max) reflectance changes.

Appendix Table 1. Parameters applied to (A) European Leaf-toed Geckos (*Euleptes europaea*) and (B) the digital camera for standardized dorsal photographs. The photographs were taken using the portable photographic studio illustrated in Figure 2.

	Parameters	Indications/Values
(A) European Leaf-toed Geckos		
	Angle of view	Back view
	Position of the animal	Horizontal
	Holding	By the posterior legs and/or the anterior legs
(B) Digital camera (Olympus® TG-6)		
	Distance between the lens and the animal	7 cm
	Macro	Yes
	Flash	No
	ISO	200
	F-number	F/2.3
	White balance	Automatic
	Resolution	300 pixels/inches minimum
	Image size	4000 x 3000
	Registration format	RAW converted to TIFF and JPEG
	Additional equipment	LG-1 LED ring (for diffused and constant light)

Appendix Table 2. Reflectance values of image pairs illustrating minimum and maximum reflectance differences for each of the 30 European Leaf-toed Geckos (*Euleptes europaea*) kept in captivity for 4 d. The absolute value of the difference (|Δ|) between the two reflectance values for each pair is provided.

	Reflectance values					
	Minimum reflectance pairs			Maximum reflectance pairs		
Individuals	1st image	2nd image	|Δ|	1st image	2nd image	|Δ|
1	0.241	0.233	0.008	0.241	0.095	0.146
2	0.214	0.214	0.000	0.216	0.088	0.128
3	0.279	0.286	0.007	0.310	0.171	0.139
4	0.158	0.157	0.001	0.230	0.121	0.109
5	0.224	0.230	0.006	0.302	0.145	0.157
6	0.114	0.118	0.004	0.210	0.114	0.096
7	0.239	0.243	0.004	0.153	0.243	0.090
8	0.204	0.203	0.001	0.268	0.156	0.112
9	0.119	0.129	0.010	0.264	0.119	0.145
10	0.250	0.250	0.000	0.278	0.149	0.129
11	0.208	0.205	0.003	0.208	0.106	0.102
12	0.150	0.149	0.001	0.239	0.124	0.115
13	0.180	0.180	0.000	0.265	0.102	0.163
14	0.229	0.232	0.003	0.260	0.164	0.096
15	0.212	0.212	0.000	0.222	0.155	0.067
16	0.227	0.233	0.006	0.117	0.248	0.131
17	0.190	0.185	0.005	0.237	0.125	0.112
18	0.147	0.143	0.004	0.219	0.143	0.076
19	0.238	0.238	0.000	0.302	0.162	0.140
20	0.162	0.164	0.002	0.109	0.231	0.122
21	0.092	0.101	0.009	0.092	0.226	0.134
22	0.216	0.216	0.000	0.218	0.123	0.095
23	0.224	0.226	0.002	0.100	0.234	0.134
24	0.213	0.214	0.001	0.133	0.253	0.120
25	0.209	0.198	0.011	0.251	0.154	0.097
26	0.185	0.188	0.003	0.117	0.224	0.107
27	0.162	0.159	0.003	0.098	0.176	0.078
28	0.216	0.215	0.001	0.110	0.232	0.122
29	0.188	0.194	0.006	0.101	0.194	0.093
30	0.234	0.233	0.001	0.234	0.127	0.107